

The phylogeny, classification and evolution of parasitic wasps of the subfamily Ophioninae (Ichneumonidae)

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Synopsis

An attempt is made to reconstruct the phylogeny of the genera of the ichneumonid subfamily Ophioninae using both parsimony and compatibility methods of analysis. The problems of phylogenetic analysis of highly homoplastic data are discussed and the strengths and weaknesses of the various methods evaluated. It was concluded that there is no wholly adequate objective method of analysing highly homoplastic data, but it is suggested that analysis may be undertaken using subjective evaluation of characters supporting conflicting patterns. Within the Ophioninae five major evolutionary lineages are recognized, the *Ophion*, *Sicophion*, *Eremotylus*, *Thyreodon* and *Enicospilus* genus-groups. The largest, the *Enicospilus* genus-group, is subdivided into five subgroups, the *Orientospilus*, *Ophiogastrella*, *Stauropactonus*, *Leptophion* and *Enicospilus* subgroups. A scenario for the possible evolution of the subfamily is suggested. Thirty-two genera are recognized, one of which, *Janzophion*, is described as new. *Rictophion* is treated as a synonym of *Euryophion*, *Ophionopsis* is treated as a synonym of *Dictyonotus*, and *Aulophion* treated as a synonym of *Stauropactonus*. The majority of genera are shown to be holophyletic, but *Ophion* and *Enicospilus* are thought to be paraphyletic, though for purposes of classificatory convenience they are retained as valid genera. Diagnostic descriptions of the genera are given and the inter-relationships of their component species are discussed.

Introduction

Ophionines are mostly quite large, slender, orange-brown ichneumonids that can frequently be observed flying around lights at night in virtually any part of the world. In temperate regions there are rather few species, but in the tropics there are very large numbers of taxa, and ophionines form a conspicuous component of the ichneumonid fauna. Almost all members of the subfamily are nocturnal or crepuscular, though in drier areas a few are diurnally active. Males of many species fly at dusk, but most females are not active until an hour or two after dark.

Ophionines are solitary protelean endoparasites of holometabolous insect larvae. The hosts of the vast majority of species are not known, but what records there are usually refer to species parasitizing lepidopterous larvae, most often exposed, solitary larvae, and in particular species of the families Noctuidae, Geometridae and Lymantriidae. Larvae of a wide range of other families are also attacked, but there are extremely few records of ophionines parasitizing Microlepidoptera or Rhopalocera. One Nearctic species is exceptional in that it is known to parasitize coleopterous larvae (Townes, 1971).

Oviposition is usually into the host larva. The parasitoid egg is apparently free in the host's haemocoel where it hatches to produce a caudate first instar larva (Moutia & Curtois, 1952). Species attacking mature larvae undergo rapid development, but species (e.g. *Enicospilus americanus*) that oviposit in very young larvae have a protracted first larval instar (Price, 1975). Several species are apparently host specific (Janzen, pers. comm.), whilst others (e.g. *Thyreodon atriventris*) parasitize a variety of taxonomically related hosts. Some temperate species seem to attack a number of different hosts in a similar niche, whilst a few species are bivoltine, with different generations attacking different hosts (Brock, 1982). A few species seem to attack a wide range of hosts (Gauld & Mitchell, 1981). The parasitoid larva completes development just prior to host-pupation, often after the host has constructed a cocoon. The ichneumonid larva spins a characteristic fibrous, ovoid cocoon which is generally dark brown with a pale equatorial band. Species may remain as mature larvae or even adults in this cocoon for the greater part of the year in seasonal habitats.

The research potential of Ophioninae

The ease with which ophionines may be collected (using m.v. light-traps) makes them particularly suitable for zoogeographic and ecological study. Large samples may be collected in terrain where sweep netting and Malaise trapping yield poor results, or, as in the case of rain forest canopy, where collecting can only be achieved by cumbersome, expensive and (for fast-flying insects) unproven techniques. Unlike Lepidoptera, which are similarly easy to collect, most tropical ophionines are readily separable without recourse having to be made to time-consuming genitalic preparation. Illustrated keys are available to facilitate identification of most Old World tropical species (Gauld, 1977; Gauld & Mitchell, 1978; 1981).

The aim of the present work

If the Ophioninae is to be used as a serious vehicle for zoogeographic study then it is necessary to have an understanding of the phylogenetic inter-relationships of the genera, as many authors contend that biogeographic speculations are valid only when related to the evolutionary history of a group (Mackerras, 1962; Nelson & Platnick, 1981). As little has been published on the phylogeny of Ophioninae, a cladistic study of the group is necessary before much of the distributional data available can be interpreted in an evolutionary manner. The aim of the present study is to investigate the phylogeny of the Ophioninae using a variety of modern cladistic techniques, and to relate the results to what is known about the distribution and biology of the group in general.

Terminology

The morphological terminology in this work follows that proposed by Richards (1956) and interpreted for the Ophioninae by Gauld & Mitchell (1978; 1981). Specialist terms, relevant to only some ophionines, are defined in these works. Family-group names used conform with the directives of the *International Code of Zoological Nomenclature* and with various *Opinions* of the International Commission. Some recent authors (e.g. Townes, 1969; 1971) have chosen to disregard certain of these opinions and have not followed the *Code* when forming family-group names (see Fitton & Gauld, 1976).

Material examined

The majority of specimens examined are contained in the collections of the British Museum (Natural History) (BMNH), but valuable additional material was furnished by the Australian National Insect Collection (ANIC), Canberra, the Bernice P. Bishop Museum (BPBM), Hawaii, the Canadian National Collection (CNC), Ottawa, the Gupta Collection (GC), the Musée Royal de l'Afrique Centrale (MRAC), Tervuren, the Muséum National d'Histoire Naturelle (MNHN), Paris, the Taiwan Agricultural Research Institute (TARI), Taichung, the Townes Collection (TC), Ann Arbor, the United States National Collection (USNM), Washington and the Zoological Institute (ZI), Leningrad. The types of virtually all Old World species have been examined and exhaustive lists of material examined are contained in recent revisionary studies (Gauld, 1977; Gauld & Mitchell, 1978; 1981; Gauld & Carter, 1983).

Discussion of methodology

The present work is an attempt to elucidate the phylogeny of the Ophioninae and therefore only phylogenetic methods of data analysis have been used. These methods are based on ideas initially expounded by Hennig (1966). Although Hennig made a major contribution to systematic philosophy, he greatly underestimated the difficulty that would occur in phylogenetic analyses due to morphologically undetectable evolutionary parallelism and character-state reversal (i.e. homoplasy). Such events result in there being incompatible character sets in taxonomic data. An estimation of the extent of incompatibility can be made using the simple test

outlined by Le Quesne (1969) (see also Gauld & Mound, 1982; Underwood & Gauld, in prep.), and such incompatibilities are far from uncommon in most real data.

In the past decade two main approaches have been adopted by cladists in an attempt to resolve conflicting character sets – parsimony methods, which seek to minimize the number of character-state transformations, and compatibility methods, which seek to find a series of nesting groups supported by the largest number of compatible characters (Felsenstein, 1982). For simple data sets where there is a low incidence of homoplasy, these methods yield very similar results (e.g. Gauld, 1983), but as the frequency of homoplasy increases so the methods usually give increasingly different results.

Parsimony methods have gained wide acceptance in the literature, with the shortest rooted Wagner tree often being uncritically presented as the best phylogenetic hypothesis. Simultaneously, many authors have criticized compatibility analysis either for producing numerous apparent best solutions (Kluge, 1976), or as being less useful at producing congruent phylogenies from different developmental stages (e.g. Mickevich, 1978; Rohlf & Sokal, 1980) (but see also Rohlf *et al.*, 1983). However, Felsenstein (1981; 1982) stated that both methods can be justified as maximum likelihood methods, but under somewhat different circumstances. If homoplasy is expected to be scattered at random throughout all characters then a parsimony method is favoured, but if homoplasy is expected to be concentrated in certain characters then compatibility is supported. Felsenstein (*op. cit.*) continues by noting that both methods require both homoplasy to be rare and characters to have a low rate of change. In the case of Ophioninae, homoplasy demonstrably is not rare, suggesting results obtained by either method should be viewed circumspectly. The additional assumption necessary for parsimony methods to approach maximum likelihood, that is that homoplasy is randomly scattered across all characters, contradicts the consensus of opinion of most practising entomological taxonomists. Both parsimony and compatibility methods were used, with caution, in this study.

Choice of parsimony method utilized

Of the parsimony methods available at the start of this study, the program selected was PHYLIP (package for inferring phylogenies) written by Dr J. Felsenstein. This program offers four routines for dealing with non-polymorphic, discrete state data: (a) the Camin-Sokal parsimony method; (b) the Dollo parsimony method; (c) the Wagner parsimony method and (d) a mixed method allowing a, b or c to be specified for each character. The Camin-Sokal and Dollo methods were not used in the present study. Neither gives as short a tree as that obtained by the Wagner method as both place additional constraints on the 'tree-growing' method (Felsenstein, 1982), the former by not allowing reversal, the latter by not permitting forward parallelism.

In the insects being studied there is virtually no evidence at all for either of the additional *a priori* assumptions these methods necessitate. Indeed there is some biological evidence to suggest that these extra assumptions are unwarranted for ichneumonids. Dollo parsimony may justifiably be invoked for treating complex structures (such as the vertebrate eye), but virtually all characters used in the present study involve small changes in simple structures. Very often the derived state involves reduction of a structure, and observation of other ichneumonid taxa suggests that certain of these apomorphies (such as reduction of extent of occipital carina) have been developed in parallel in numerous different evolutionary lineages. Even when the apomorphic state is the development of a novel structure (such as an alar sclerite), the evidence strongly suggests (as the feature occurs in a few otherwise specialized species of several different genera) parallel development in closely related lineages.

Reversal is more difficult to demonstrate, but clearly it does occur. For example, the alar sclerites apparently have been lost by some *Enicospilus* species on oceanic islands (Gauld & Carter, 1983) and the posterior transverse carina of the propodeum, which is absent in most *Enicospilus* species, has been redeveloped in some members of the otherwise highly specialized *E. signativentris* species-complex (Gauld & Mitchell, 1981).

Because of the objections to the Camin-Sokal and Dollo methods the option employed in this study was that which necessitates no extra *a priori* assumptions, the Wagner method. Clado-

grams were rooted using a hypothetical all zero ancestor, as use of any outgroup taxon is liable to introduce more incidences of homoplasy.

The advantages and disadvantages of the parsimony method

The major advantage of the parsimony method seemed to be that, because of its 'averaging procedure' (see below), generally all species of a particular genus were associated. As ophionine genera are polythetic, compatibility methods invariably exclude certain taxa (see Davies & Boratyński, 1979).

Despite its widespread acceptance there are serious flaws in parsimony methodology when applied to complex data sets. (There are also philosophical objections (see Pratt, 1972; Felsenstein, 1981; Friday, 1982; Panchen, 1982), but these are beyond the discussion of the present work.) One, and perhaps the most obvious methodological flaw, is that because the method considers each character as an identical piece of binary information, and is attempting only to minimize transformation, a large set of coincidental 'bad' characters will be favoured at the expense of even a very slightly smaller set of 'good' characters. This is best illustrated in the case of some Hawaiian genera of ophionines (taxa 924-6 in the following study) and *Ophiogastrella* (taxa 910-11). In both cases, the sets of characters responsible for positioning these taxa in the Wagner analysis are composed of characters that are likely to be highly homoplastic in other taxa. Although a traditional taxonomist intuitively recognizes these as poor characters (and taxonomist's intuitive judgement may be very good, see Davies, 1981) and has no confidence in them as indicators of phylogenetic affinity, it was not found to be possible to translate this subjective bias into an objective taxonomic weighting scheme. Without an objective weighting scheme the averaging procedure adopted by the Wagner method has the effect of reducing the number of transformation steps of many 'weak' characters at the expense of 'moderately good' ones (Strauch, 1984).

Although some hybrid parsimony/compatibility trees produced in this study were longer than the shortest Wagner tree (mainly because certain characters appear to have been 'written-off', i.e. allowed to have a large number of transformations) it is noteworthy that these cladograms were supported by more characters with minimal or nearly minimal homoplasy. This can best be illustrated by reference to two alternative cladograms produced during this study, the most parsimonious 235-step one and the favoured 239-step one (Gauld, unpubl. PhD). The numbers of characters with various numbers of transformation steps are shown in Fig. 1.

A second disadvantage of the parsimony method is that a multiplicity of almost equally parsimonious cladograms may be generated from the same data set by the same procedure (Strauch, 1984), but altered merely by re-ordering the input order of the taxa (e.g. Figs 21-24). In this study it soon became apparent, when rearrangements are practised, that certain taxa are prone to 'hopping', i.e. moving from one lineage to another in different reconstructions. Taxon 906 was found to be such an OTU - its final position in a cladogram depended solely upon the position in which it was entered into the analysis. This was presumed to operate in the following manner: taxon 906 is almost equally associated (see Appendix 3) with three separate lineages, *Simophion*, the *Thyreodon* complex and the *Enicospilus* complex. This equality of association is so pronounced that once the taxon has linked to one or other of the alternatives (the first encountered) it does not share enough derived features with any other taxon to disassociate itself. Thus if the first three taxa entered are 905 (*Simophion*), 906 and 940 (a more distantly related taxon), 906 remains associated with 905, whilst if the first three taxa entered are 935 (one of the *Thyreodon* complex), 906 and 940, 906 remains associated with the *Thyreodon* complex. Some programs attempt to circumvent this problem by computing an 'advancement index' for ordering the taxon input, but I fail to see the intellectual justification for this.

A third disadvantage of the parsimony method is that it is not possible to predict, from any given data set, the actual minimum tree length (Felsenstein, 1982; Day, 1983). This means that, for large data sets, in practice one is guessing that the minimum length tree obtained is the shortest possible. This study shows that for highly homoplastic data, a number of equally short, quite different cladograms may be obtained. It appears to be merely an *act of faith* that a slightly

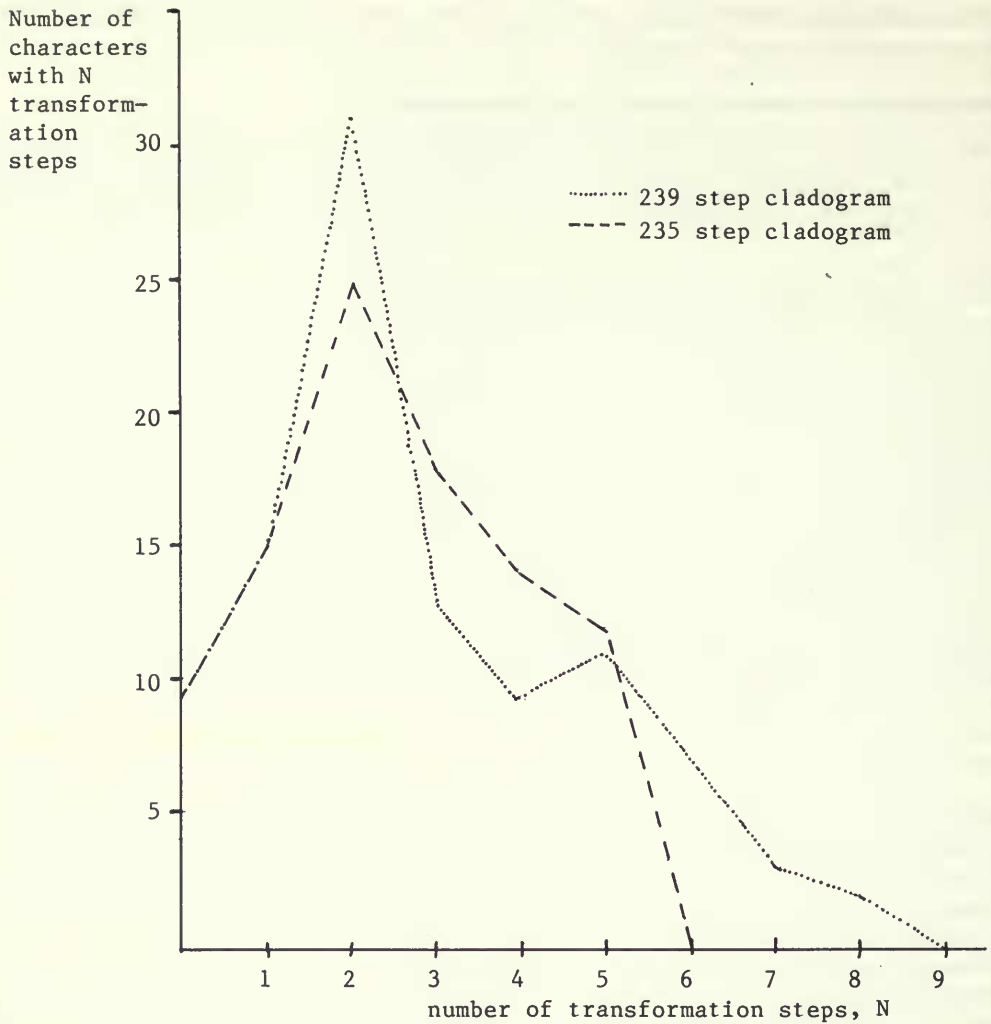


Fig. 1 A comparison of the incidences of transformation required to fit all characters to the most parsimonious 242-step cladogram and a favoured 249-step cladogram (From Gauld, unpubl. PhD thesis). It is noteworthy that the latter, although 7 steps longer, is supported by more minimally homoplastic characters.

shorter and yet totally different arrangement does not exist, a rather disconcerting observation if one accepts the principle of parsimony as paramount in phylogenetic reconstruction.

Compatibility methods utilized

Felsenstein's package, PHYLIP, provides an option for producing compatible character sets. This option, CLIQUE, was used to find the largest cliques for various sets of taxa considered in this study. A second program (written by Dr G. Underwood) was developed by Underwood and Gauld during the course of this study. This program was developed from the work of Le Quesne (1969; 1972) and involves calculating the probability of incompatibility between two characters on a null hypothesis of random distribution of states of both. This value was then used to calculate for each character a coefficient of character-state randomness (herein called the O/E value). Typically the output of this program, LEQU.BAS, consists of a list of characters with their observed incompatibilities, calculated expected number of incompatibilities, and O/E

values tabulated; the characters are ranked by O/E value as a postscript (e.g. Tables 2, 6). A facility has been incorporated so that multistate characters which have been coded in binary fashion and numbered as decimal increments (e.g. 1.1, 1.2), and cannot logically fail, are not compared.

Included also in LEQU.BAS is a labelling feature. This is based on an idea given by Guise *et al.* (1982) for counting frequencies of each of the four possible character-state combinations (0,0; 0,1; 1,0; 1,1) for each character pair. If a pair of characters fail the test (because all four combinations are found in the data) on account of a single occurrence of one combination, the taxon having this combination is labelled. The results of this operation are printed in the form of a table (e.g. Appendix 4). The figure in brackets adjacent to the taxon is the total number of labels the taxon has received. The taxa most frequently labelled will be the ones with the most discordant character sets. A particularly high label score for a species for any one character strongly suggests homoplasy for that character with respect to other taxa in the set. Some care is needed in the interpretation of results as characters with very unequal character-state distribution (either only two 0 or two 1 scores) often have high label values. These are easily recognized as equally high scores are given for the two taxa with the minority states. Even these values can sometimes be seen to be unusually high (i.e. suggestive of homoplasy) if the character label values are compared with the label values of similarly uninformative characters.

Value of LEQU.BAS for overcoming some problems of compatibility analysis

Two major disadvantages with compatibility analysis are: (1) a maximum character set is often far too small to allow full resolution of data (Felsenstein, 1982) and (2) the data set may yield a number of more or less equally large cliques (Kluge, 1976). LEQU.BAS is of some value in overcoming both these problems.

As the largest compatible character set is generally very small, it is useful to have a way of ordering characters. Homoplastic characters that would be eliminated from any compatible set are not all equally bad; some are far more discordant than others. For example, allowance of just one incidence of parallelism or reversal may be enough to make certain characters compatible with a cladogram, whereas others will necessitate the invocation of multiple incidences of homoplasy to achieve congruence. It can be seen from the hypothetical data set 1 (Tables 1-3) that LEQU.BAS offers a way of grading characters from slightly to extremely homoplastic. Eight taxa, A-H, exhibit 18 binary characters (Table 1). Characters 1-12 support the nested set (((AB)C)((DE)(F(GH))))). Characters 13-18 are differentially homoplastic, 13 and 14 requiring one extra transformation to fit the specified cladogram, 15 and 16 requiring two extra transformations and 17 and 18 needing three extra. Analysing these data with LEQU.BAS gave the results presented in Table 2. It can be seen that the six homoplastic characters are ranked in order of the extra number of transformations required to make them fit the specified cladogram. Several taxa are highly labelled for certain characters, suggesting homoplasy. For example, character 15, which is present in the apomorphic state in B and C, but is plesiomorphic in A, is highly labelled for A, suggesting a reversal may have occurred.

Table 1 Character state matrix for hypothetical data set 1. A-H represent taxa, 1-18 their independent characters. 0 = plesiomorphic, 1 = apomorphic.

| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 |
|---|---|---|---|---|---|---|---|---|---|----|----|----|----|----|----|----|----|----|
| A | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 |
| B | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 1 |
| C | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 |
| D | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 |
| E | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 |
| F | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 |
| G | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 |
| H | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 1 |

Table 2 Result of LeQuesne test on hypothetical data set 1. The number in italics is the character number, the second column is the number of observed failures, the third column the number of expected failures and the final column in each case the ratio of observed over expected failures. Characters with a low O/E value are considered to be good characters, and are ranked in the final line higher than those with high O/E scores.

| Character number: | | | | failures observed | expected | O/E ratio | | | | | | | | | | | |
|-------------------|----|-------|------|-------------------|----------|-----------|------|-----------|----|-------|------|----|----|----|----|----|----|
| <u>1</u> | 3 | 8.68 | 0.35 | <u>2</u> | 3 | 8.68 | 0.35 | <u>3</u> | 5 | 12.21 | 0.41 | | | | | | |
| <u>4</u> | 5 | 12.21 | 0.41 | <u>5</u> | 5 | 12.21 | 0.41 | <u>6</u> | 5 | 12.21 | 0.41 | | | | | | |
| <u>7</u> | 2 | 8.68 | 0.23 | <u>8</u> | 2 | 8.68 | 0.23 | <u>9</u> | 4 | 12.21 | 0.33 | | | | | | |
| <u>10</u> | 4 | 12.21 | 0.33 | <u>11</u> | 3 | 8.68 | 0.35 | <u>12</u> | 3 | 8.68 | 0.35 | | | | | | |
| <u>13</u> | 7 | 12.21 | 0.57 | <u>14</u> | 8 | 13.09 | 0.61 | <u>15</u> | 10 | 12.21 | 0.82 | | | | | | |
| <u>16</u> | 13 | 13.09 | 0.99 | <u>17</u> | 16 | 13.09 | 1.22 | <u>18</u> | 16 | 12.21 | 1.31 | | | | | | |
| Grand totals- | | | | failures observed | expected | O/E ratio | | | | | | | | | | | |
| | | | | 57 | 100.63 | 0.57 | | | | | | | | | | | |
| Ranking ratios | | | | | | | | | | | | | | | | | |
| 7 | 8 | 9 | 10 | 1 | 2 | 11 | 12 | 3 | 4 | 5 | 6 | 13 | 14 | 15 | 16 | 17 | 18 |

Although there is a clear relationship between the number of extra transformations required to make a character 'fit' a favoured cladogram and that character's O/E value, the O/E value also varies with information value of the character, i.e. the number of 1 scores in relation to 0 scores. For example, in data set 1, character 14 may be modified so it has the following distribution of 1 states in taxa A-H, 11100000, 11001000 or 10001001. These require one, two and three transformations, respectively, and have O/E values of 0.41, 0.90 and 1.24. However, if the number of transformations necessary is kept constant (at say two) and the number of derived states varied, the following relationship may be observed: 10001000 (O/E = 1.41), 11001000 (O/E = 0.90), 11011000 (O/E = 0.61), 11100010 (O/E = 0.53), 11100011 (O/E = 0.50), 11100111 (O/E = 0.23). Similar variations of character 16 (requiring three transformations) produced values with the range 0.74-1.24 (the largest being for 10010001), whilst a range of 1.16-1.35 was found for a character requiring four transformations. Thus a homoplastic character with a high proportion of derived states supporting various subgroups in the definitive cladogram may have a lower O/E value than a less homoplastic, but less informative character.

Kluge (1976) pointed out that compatibility analysis may produce a large number of equally large cliques. From his data set of 139 binary characters he obtained six almost equally large cliques of 80 or 81 characters. Kluge remarked that not only is there no reason to prefer one to any other of the sets, but also pointed out that the most primitive species in each of the cliques did not correspond to the most primitive as assessed on the basis of the best documented characters. To consider Kluge's objections necessitates re-examining his data. Of his six largest cliques, it is apparent that no less than 76 characters are common to all sets. The six dendrograms supported by these cliques are essentially similar, differing mostly in the relative order of the most primitive taxa (im-ti in Kluge's fig. 7a) so a great deal of information is common to all, and

Table 3 Labels matrix derived from hypothetical data set 1. The column to the right of the taxon letter is the total number of times that taxon is solely responsible for a character failing the LeQuesne test. For further details see text.

| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 |
|--------|---|---|---|---|---|---|---|---|---|----|----|----|----|----|----|----|----|----|
| A (21) | 3 | 3 | 3 | 3 | 3 | 3 | - | - | - | - | - | - | 1 | - | 8 | 2 | 6 | 7 |
| B (6) | 3 | 3 | - | - | - | - | - | - | - | - | - | - | - | - | 2 | - | 2 | 2 |
| C (8) | - | - | 2 | 2 | 2 | 2 | - | - | - | - | - | - | 4 | - | 4 | - | - | |
| D (5) | - | - | - | - | - | - | 2 | 2 | - | - | - | - | 1 | - | - | - | 2 | 3 |
| E (7) | - | - | - | - | - | - | 2 | 2 | - | - | - | - | 1 | - | 2 | - | 4 | 3 |
| F (5) | - | - | - | - | - | - | - | - | 1 | 1 | - | - | 5 | 1 | 1 | 1 | - | - |
| G (12) | - | - | - | - | - | - | - | - | 2 | 2 | 3 | 3 | - | 1 | 1 | 4 | 2 | 6 |
| H (8) | - | - | - | - | - | - | - | - | 1 | 1 | 3 | 3 | - | - | - | 2 | 4 | 2 |

this agrees with Kluge's preferred phylogenetic arrangement. Most of the differences between cliques (and between the dendrograms supported by these and the preferred arrangement) involve relatively uninformative characters. It is mathematically demonstrable that the probability of chance compatibility of a particular character with any other set of characters is inversely proportional to the information value of the character. Therefore, one criterion of which clique to select is to favour that with the highest information value.

However, in practice one frequently finds that the subsets which are not common to all the similar-sized cliques comprise equally poorly informative characters. In such cases the average O/E value for a clique is a useful indicator of the degree to which the clique is consistent with slightly homoplastic (and hence excluded) characters which are not normally considered in a compatibility analysis. For example, consider the hypothetical data set 2 (Tables 4, 5). There are two equally large, equally informative cliques:

- A (10) [1, 2, 3, 4, 5, 6, 7, 8, 9, 10] Average O/E value = 0.308
- B (10) [1, 2, 3, 4, 5, 6, 7, 8, 9, 14] Average O/E value = 0.323
- $A \cap B = \{1, 2, 3, 4, 5, 6, 7, 8, 9\}$

Table 4 Character state matrix for hypothetical data set 2. Conventions follow table 1.

| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 |
|---|---|---|---|---|---|---|---|---|---|----|----|----|----|----|
| J | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 |
| K | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 |
| L | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 |
| M | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| N | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| O | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 |
| P | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 |
| Q | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 |

Table 5 Results of LeQuesne test on hypothetical data set 2. Conventions follow table 2.

| Character number: | failures observed | expected | O/E ratio |
|-------------------|-------------------|----------------|------------|
| <u>1</u> : 3 | 9.86 0.30 | <u>2</u> : 3 | 9.86 0.30 |
| <u>4</u> : 3 | 9.86 0.30 | <u>5</u> : 3 | 10.63 0.28 |
| <u>7</u> : 3 | 9.86 0.30 | <u>8</u> : 3 | 9.86 0.30 |
| <u>10</u> : 1 | 6.89 0.15 | <u>11</u> : 11 | 9.86 1.12 |
| <u>13</u> : 12 | 10.63 1.13 | <u>14</u> : 4 | 6.89 0.58 |

Ranking ratios
 10 6 5 9 1 2 3 4 7 8 14 11 12 13

These sets differ in one character, possession of either 10 or 14. Character 10 supports J + K whereas 14 supports J + M. No other character that is compatible offers support for one or other of these alternatives but some homoplastic characters do support J + K (plus other taxa also) reinforcing the J + K grouping suggested by character 10. No homoplastic character reinforces the J + M suggestion. This reinforcement can be detected by differences in the values of the O/E ratio, as character 10 scores 0.15 whereas character 14 scores 0.58. This difference in O/E value is responsible for the difference in average O/E values of the two cliques A and B, and it thus seems reasonable to prefer the clique with the lowest average O/E value. This method offers a simple objective procedure for selecting one of a number of large cliques as 'most favourable', as it will be the one reinforced by most secondary characters.

In the present study compatibility analysis was found to give, up to a point, results that were similar to conventional taxonomic assessment. Frequently, characters considered important in generic classification by traditional taxonomists were found to be the intersect of the largest cliques.

The operational procedure adopted in this study

This study was commenced by tentative recognition of groups of taxa from the shared derived character matrix (Appendix 3). The rigidity of these groups was tested using Underwood's FOURS program (Underwood, 1982) and then further analyses using the compatibility and parsimony methods outlined above. Resulting cladograms were compared and differences subjectively evaluated by appraisal of characters supporting different options. The various groups were gradually related to each other until the majority of taxa had been placed. The remaining unplaced taxa all exhibited confusing affinities. To facilitate their placement a number of hypothetical taxonomic units were proposed to represent the various genera already placed in the analysis. The data set comprising hitherto unplaced taxa and HTUs was analysed using parsimony and compatibility techniques, and the resulting cladograms subjectively evaluated.

An apologia for subjectivity in cladistic analysis

In recent years there has been a great deal of intellectual activity devoted to making taxonomy more 'scientifically respectable' by attempting to remove subjectivity. Phenetic methods were the first to be claimed as objective taxonomic procedures (Sokal & Sneath, 1963), but these methods were essentially a movement away from evolutionary taxonomy (Nelson & Platnick, 1981) and have largely been eclipsed by the development of numerical cladistics. Despite the seeming objectivity of such numerical methods, they are really only objective ways of analysing largely subjective data, as character selection is a highly subjective procedure (Pratt, 1972). Furthermore, the claim by many cladists that their favoured numerical methods (parsimony analyses) are scientific (in the Popperian sense) is flawed by the assumption that parsimony *per se* is a criterion for formulation of a scientific hypothesis (i.e. the least falsified hypothesis is accepted – Gaffney, 1979), as is eloquently shown by Panchen (1982). A phylogenetic hypothesis derived from a cladistic analysis rests on the supposition (or hypothesis) that a particular derived character-state is a genuine synapomorphy which thus indicates commonality of descent of two or more taxa. In a highly homoplastic data set, for every character that is accepted as a genuine synapomorphy, others are rejected as showing false patterns. Farris (1969) defends parsimony in such cases, on the grounds that hierarchic correlations are more likely to occur among cladistically reliable characters than among cladistically unreliable characters (i.e. random variables). This is true only if cladistically unreliable characters vary randomly and is not a corollary of the generally accepted statement that random variables are cladistically unreliable characters. Clearly it is untrue; most taxonomists can cite examples of suites of characters being size related, habitat related, associated with a particular biological strategy and so forth. How then is a taxonomist supposed to choose between competing character sets if not by 'biggest is best' criteria? I think this can only be done at present, subjectively. Competing character sets are examined in the light of a taxonomist's knowledge of the variability of characters over a much wider group of organisms. Highly variable features (such as the number of ribs or vertebrae in some birds – Strauch, 1984 – or the form of mammalian teeth – Butler, 1982) are rejected as unlikely to be indicative of phylogenetic affinity. Other sets clearly comprise adaptive features associated with certain habitats and these may likewise be rejected. It is noteworthy that very many cladistic analyses seem to have been undertaken on data sets that have initially been subjectively edited (with no explanation) by discarding characters which are presumably thought to have no phylogenetic value. In this work I have tried to explain my reasons for rejecting certain character sets in preference to others.

The holophyly of the subfamily

A prerequisite to meaningful cladistic analysis is the establishment of the holophyly of the group being studied. The holophyly of the Ophioninae is supported by the following apomorphies.

(a) Possession of a spurious vein extending from the vannal notch to the tornus of the fore wing. This feature, first recognized by Perkins (1959), is an autapomorphy of the subfamily.

- (b) Possession of numerous setae on the labial sclerite of the final instar larva (Short, 1978). This feature is also an autapomorphy of the subfamily.
- (c) Presence of a single radio-medial cross vein (? $3r-m$) far distal to $2m-cu$. This unusual condition is elsewhere only found in isolated genera of the Campopleginae, Tersilochinae and Anomaloniinae (Townes, 1970; 1971; Gauld, 1976). In none of these taxa is the cross vein as far distal to $2m-cu$ as is the case in ophionines.
- (d) Possession of a sinuous pectinal comb on the tarsal claws. Many ichneumonids have a few scattered pectinal teeth on the tarsal claws but very few have a strongly developed sinuous comb like that found in virtually all ophionines.
- (e) Total loss of gymmae. These structures are present in at least some members of virtually all other subfamilies. No trace has ever been observed in ophionines.
- (f) Enlargement of ocelli and related nocturnal specializations (Gauld & Huddleston, 1976). The pale colour, enlarged ocelli and eyes, long antennae and slender legs are features found in many nocturnal ichneumonoids, but this suite of characters is apparently an apomorphic feature of the Ophioninae.

The systematic position of the subfamily

The subfamily Ophioninae belongs to the Ichneumonidae, a holophyletic group of apocrite Hymenoptera (Königsmann, 1978). Virtually nothing has been published about the phylogenetic relationships of ichneumonid taxa and, if a reasonable assessment is to be made of character polarity in Ophioninae, it is necessary to attempt to place the group in relation to some other subfamilies.

From study of Cretaceous fossil ichneumonoids (Townes, 1973a & b; Rasnitsyn, 1983), comparison with putative ancestral groups (such as siricids and cephids) and examination of primitive extant Apocrita (e.g. Megalynidae, Stephanidae, some Braconidae), it can be deduced that primitive ichneumonoid features are likely to include: possession of an un-notched (possibly long) ovipositor; possession of a gaster that is broadly attached to the propodeum and has a free first sternite; possession of an areolated propodeum; possession of notaular grooves; possession of simple or basally lobate claws. Study of the biological evolution of parasitoids (e.g. Shaw, 1983) suggests that the ectoparasitic habit is primitive with respect to endoparasitism, and as both types occur in the Ichneumonidae (Clausen, 1940; Gauld, 1984b), one expects that the most primitive taxa will be found amongst ectoparasitoids. Some authors (e.g. Cushman, 1926; Telenga, 1969; Achterberg, 1976; 1984) suggest that primitive ichneumonoids are likely to have been parasites of xylophagous coleopterous larvae, as are archaic extant parasitoids such as orussids (Quinlan & Gauld, 1981; Middlekauf, 1983). These data suggest that the most primitive extant ichneumonids are to be found amongst the Pimplinae, Labeninae and perhaps also Tryphoninae. This hypothesis is supported by studies of larval morphology (Short, 1978) and is concomitant with the informal higher classificatory scheme outlined by Townes (1969).

Compared with the Pimplinae and Labeninae, the Ophioninae appears to be a rather specialized subfamily. It seems to belong to a large, holophyletic group of taxa that includes the subfamilies Ophioninae, Campopleginae, Cremastinae, Tersilochinae, Banchinae and Ctenopelmatinae. The holophyly of this group is suggested by the following apomorphies:

- (a) possession of a dorsal subapical notch on the ovipositor;
- (b) possession of similar female reproductive tract (Pampel, 1913);
- (c) having endoparasitic larvae which lack a labral sclerite and possess a Y-shaped prelabial sclerite (see also Fig. 2).

Two of the included taxa, the Ctenopelmatinae and Banchinae, usually possess a plesiomorphic first gastral segment which is broadly attached to the propodeum, has a more or less centrally positioned pair of spiracles and a free sternite. In the Ophioninae, Campopleginae, Cremastinae and Tersilochinae this segment is specialized. It is more slender, has the tergite and sternite intimately fused and is lengthened anteriorly so that the spiracles are nearer to the posterior end. Furthermore, all these taxa possess apomorphic, laterally compressed gasters, suggesting they constitute a holophyletic clade.

Within this clade two apparent groups are recognizable. One comprises the Tersilochinae + Cremastinae and is supported by two apomorphies, possession of an enlarged pterostigma and strongly shortened vein *Rs* in the hind wing. In addition both these taxa share a number of developmental trends (underlying synapomorphies of Saether, 1979), most notably, the development of a sinuous ovipositor apex and the presence of dorsally convergent eyes in males. The second group, Ophioninae + Campopleginae, is supported by a larval specialization, the possession of an expanded labial sclerite. The petioles of these two taxa are similarly modified, although this development appears to have been paralleled in some tersilochines (primitive tersilochines have a more 'cremastine-like' petiole). Most ophionines and campoplegines possess an apomorphic short, straight ovipositor; even when it is long it is very similar in the two groups, being robust and up-curved.

For the purposes of this study the Ophioninae is considered to be the sister-group of the Campopleginae, and the Campopleginae + Ophioninae is treated as the sister-group of the Cremastinae + Tersilochinae (Fig. 2).

Polarity determination and character coding

The polarity of the majority of characters has largely been determined by the method of out-group comparison (Watrous & Wheeler, 1981) using as out-groups the taxa mentioned above. Unfortunately this method does not work for all characters, usually because both states occur in both the group under study and the out-groups. In these cases the polarity assignment is based on unsatisfactory criteria such as common equals primitive, but this is stated in the discussion.

In many cases in the Ichneumonidae, character-states are progressive steps in the loss of ancestral features such as the occipital carina, propodeal carinae or segments of the palp. Such characters can be arranged in simple transformation series, from plesiomorphic to the most derived state. For example, for maxillary palps – 5-segments to 4-segments to 3-segments. Such transformation series may simply be scored in binary form as two characters –

| | | |
|----------------------------|-----|-----|
| | 8·1 | 8·2 |
| maxillary palp 5-segmented | 0 | 0 |
| maxillary palp 4-segmented | 1 | 0 |
| maxillary palp 3-segmented | 1 | 1 |

where 0 = plesiomorphic and 1 = apomorphic. Hence 8·1 represents reduction from 5 to 4 segments and 8·2 further reduction to 3. Such characters are obviously not independent for it is impossible to have a 0,1 coding as, if extreme reduction is observed, it is assumed that an intermediate stage has been passed through.

In other cases a particular structure may have been modified in one of several ways. For example, in the Ichneumonidae generally the mandible is bidentate equally, so in the Ophioninae teeth of the same length must be considered a plesiomorphic feature. Although the lower tooth is fairly constant in size, the upper may either be lengthened or shortened. Such a bifurcate series can be scored as two binary characters –

| | | |
|----------------------------|-----|-----|
| | 4·1 | 4·2 |
| mandible equally bidentate | 0 | 0 |
| upper tooth enlarged | 1 | 0 |
| upper tooth reduced | 0 | 1 |

Thus character 4·1 represents enlargement of the upper tooth, whilst 4·2 represents reduction. Clearly a 1,1 coding cannot exist for such character pairs. All transformation series in the characters dealt with below have been treated in similar fashion.

From the very large number of characters exhibited by the Ophioninae a number have been selected which show the greatest range of variation between the different genera. Included are all characters previously considered to be diagnostic of genera, and a number of additional features that have been found to be useful in delineating species-groups (e.g. in Gauld &

Mitchell, 1978). Many other characters, features in which a single species differs from others in a species-complex, were excluded from this analysis. These characters, such as the shape of the alar sclerites, form of the microsculpture of the alitrunk, density of hairs on the wing surface, general colour pattern, relative length of the mid tibial spurs etc., show a considerable range of variation within the species of any single genus and, in most cases, this range of variation is repeated in many genera. Such characters were considered to be unlikely to make significant contribution to resolving the phylogeny of the genera.

Characters used in the study

In the following section considerable space has been allocated to explaining the rationale involved in character scoring and polarity determination. Although this practice is not usual in all cladistic studies (characters are frequently relegated to an appendix) it is considered to be important in the present work. It is upon these scores that the results of any numerical analysis depend; consequently, this section is seminal to the entire work.

The characters and their polarity

- 1-1, 1-2 *Occipital carina*. A complete occipital carina is plesiomorphic (0,0). It may be centrally interrupted (1,0) or absent (1,1).
- 2 *Mandibular axis*. The plesiomorphic condition is for the axis of articulation of the mandible to be at 90° to the longest axis of the head. In a few ophionines the head is narrowed and the mandibular axis tilted almost into the vertical plane (1).
- 3 *Mandibular swelling*. A flat outer mandibular surface is plesiomorphic for ichneumonids; the swelling present near the mandibular base of some ophionines is apparently a derived feature (1).
- 4-1, 4-2 *Mandibular teeth*. The relative lengths of the teeth vary considerably in ichneumonids, but equally bidentate appears to be the plesiomorphic state (0). In ophionines the alternative specializations are – upper tooth elongate (1,0) and upper tooth reduced (0,1).
- 5-1, 5-2 *Torsion of the mandibles*. The plesiomorphic condition for ichneumonids is to have the teeth of the mandible aligned in the same plane as the mandibular axis (Figs 38, 39). Many ophionines have the mandible twisted from 5–50° so that the lower tooth is directed forwards (Fig. 40). In a few species the mandible is exceptional in being twisted more than 70° so that, when closed, the lower tooth occludes the internal, upper one. This torsion is here considered a serial development, from untwisted (0,0) through slightly twisted (1,0) to exceptionally twisted (1,1). The selective advantage of this torsion is not clearly understood, but it is suggested that it is important in facilitating egress from certain types of cocoon. It is noteworthy that not only do all species of the huge and successful genus *Enicospilus* have such mandibles, but the totally unrelated tryphonine genus *Netelia* (which is also nocturnal and has a similar host range) also has twisted mandibles.
- 6-1, 6-2 *Shape of the clypeal margin in anterior aspect*. The shape of the clypeus is often characteristic of a group of ichneumonids. For example, in the pimelines it is usually bilobate, in the anomalonines convex with a central tooth, whilst in the ichneumonines it is usually flat and truncated. The weakly convex condition found in many ophionines, campoplegines and cremastines is considered plesiomorphic. In the Ophioninae the clypeus may be modified one of two ways – either being strongly concave (1,0), or centrally produced and pointed (0,1).
- 7-1, 7-2 *Clypeal profile*. It is difficult to assign polarity to this character, but the widespread condition in the subfamily and in the closely related out-groups was assumed to be plesiomorphic. This is the possession of a virtually flat clypeus (0,0) (Fig. 39). The clypeus may be modified in one of two ways – either flared outwards (1,0) (Fig. 44) or with a groove present parallel to the margin, so that the actual margin is sharp (0,1) (Fig. 38).
- 8-1, 8-2 *Number of maxillary palp segments*. The plesiomorphic condition for the Hymenoptera is 6-segmented palps, but in the Ichneumonidae the number is reduced to 5. Fusion may occur between the distal two or three segments leading to a reduction in apparent segment number to 4 or 3. This character is scored as a transformation series, 5-segmented being 0,0, 4 being 1,0 and 3 being 1,1.
- 9 *Shape of central segments of maxillary palp*. In most primitive ichneumonids, virtually all members of the out-groups and many ophionines, the maxillary palp segments are slender and elongate. This is considered to be plesiomorphic. In a few ophionines the central segments are specialized, being globose.
- 10 *Maxillae*. The maxillae of most ichneumonids resemble those of the more primitive mandibulate

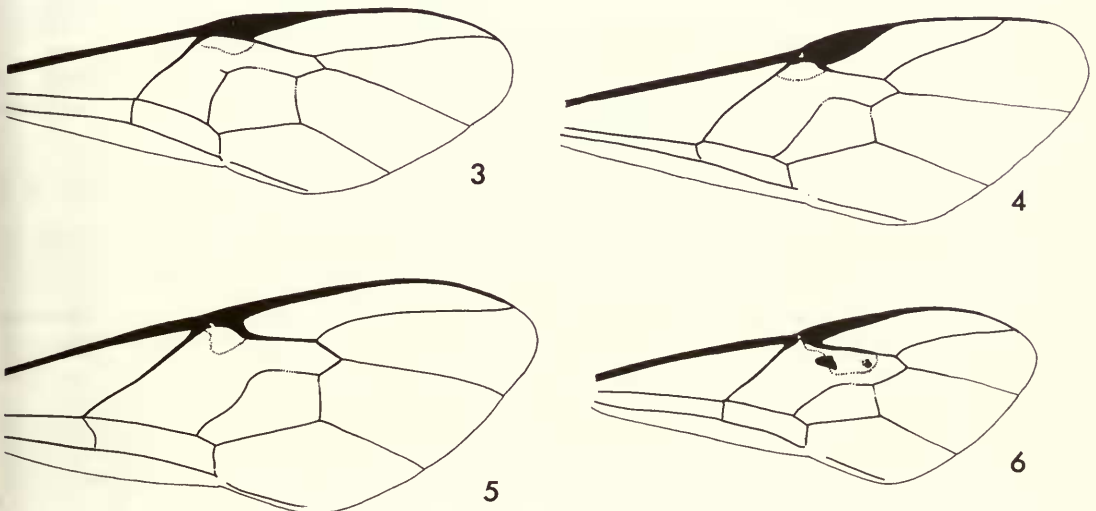
hexapods (Richards, 1956). A few ophionines have the maxillae specialized, unusually elongated so that the galea projects below the mandibles. This apomorphic condition is found in species inhabiting dry areas and is presumed to be an adaptation to feeding from certain flowers.

- 11 *Labium*. Like the maxillae, the labium is remarkably unspecialized in most ichneumonids. A few eremic ophionines possess greatly elongated glossae, an apomorphy that presumably has a similar function to character 10.
- 12 *Ocelli*. The majority of ophionines exhibit a set of features, the so-called ophionoid facies (Gauld & Huddleston, 1976), common to nocturnal Hymenoptera. These features are here regarded as apomorphies of the entire Ophioninae. They include possession of greatly enlarged ocelli. The majority of species in the out-groups, being diurnally active, lack this specialization. Consequently the possession of enlarged ocelli must, within the Ophioninae, be regarded as a plesiomorphy. In a few areas where competition from other ichneumonids is low, e.g., remote islands, deserts, tops of high mountains, several ophionines have adopted a diurnal habit. This is presumed to be a secondary feature as several species retain some nocturnal features. However, these diurnal species have small ocelli, and in these cases small ocelli are considered apomorphic. Polarity determination of this character can be questioned as it is based on an *a posteriori* inference.
- 13 *Frontal grooves*. Most ichneumonids, including almost all members of the out-groups, have the lateral part of the frons flat. In some ophionines a groove is present on either side, parallel to the inner orbit. Possession of this groove is regarded as a specialization.
- 14-1, 14-2 *Flagellum length*. In most ichneumonids the flagellum is setaceous and consists of a large number of more or less identical segments (flagellomeres). In the majority of ophionines there are between 45 and 65 such segments, and the flagellum is about as long as the fore wing. This is considered, because of its common occurrence within the group, to be the plesiomorphic condition. The flagellum appears to be modified in one of two ways. Either the segments may be very short and transverse (scored 1,0) or the number may be greatly increased (to between 75 and 95) so the flagellum is very much longer than the fore wing (0,1). A short flagellum is found in many species inhabiting hot, dry areas, and is perhaps an attempt at reducing an evaporative surface. A very long flagellum is found in species inhabiting humid areas, particularly rain forest canopies. Similarly shortened or elongated antennae can be observed in other groups, e.g. the Anomaloninae (Gauld, 1976).
- 15-1, 15-2 *Spiracular sclerite*. In most ichneumonids, including the majority of species in the closely related out-groups, the spiracular sclerite is exposed and is clearly visible near the upper hind corner of the pronotum (Fig. 42). This is considered to be plesiomorphic. A large number of ophionines have the upper corner of the pronotum somewhat broadened and notched to partially occlude the spiracular sclerite (1,0), whilst in a few species this flap completely covers the sclerite (1,1) (Fig. 43).
- 16-1, 16-2 *Notauli*. The notauli are grooves in the mesoscutum that appear to extend backwards from the anterior margin, and at their most extreme, reach the scuto-scutellar groove. The presence of these grooves seems to be a plesiomorphic feature (0,0), as they are well developed in many sawflies and are visible in many fossil apocritans. However, notauli are not present in all members of the out-groups so some doubt remains about the correct polarity of this character. The majority of ophionines only have vestigial notauli impressed at the extreme anterior margin of the mesoscutum (1,0), whilst in several they are absent entirely (1,1).
- 17 *Pronotal crest*. The plesiomorphic condition for ichneumonids is possession of a more or less flat pronotum dorsally. In several ophionines a crest is present to protect the neck region, possibly against attacks by asilids which habitually kill Hymenoptera by piercing the cervical region. The presence of this crest is regarded as an apomorphy.
- 18-1, 18-2 *Mesopleural furrow*. The plesiomorphic condition of the ichneumonid mesopleuron is for it to be relatively flat with a small pit (the episternal scrobe) near to the middle of the mesopleural suture (Townes, 1969). Amongst ophionines two specializations have apparently arisen – the presence of a diagonal groove from the pit to just below the subalar prominence (1,0) or possession of a groove from the pit to the upper end of the epicnemial carina (0,1).
- 19 *Epicnemial carina*. It is a plesiomorphic feature for ichneumonids to have this carina complete, extending laterally from the medioventral line to near the subalar prominence. In a number of taxa the lateral portion of this carina is lost (1).
- 20-1, 20-2 *Scutellar carinae*. These carinae are of sporadic occurrence throughout the Ichneumonidae but in many of the more primitive groups such as Pimplinae they are not developed. In the majority of species in the out-groups these carinae are absent, suggesting that their absence in ophionines may be a plesiomorphic feature. When present these carinae may be short, reaching to or not quite to the centre (1,0), or they may be virtually complete, reaching 0.8 or more of the length of the scutellum (1,1).

- 21·1, 21·2 *Metanotal protuberances*. The hind rim of the metanotum of most ophionines, as well as most campoplegines and cremastines, is unspecialized. In a few ophionines a small lateral tooth is discernible (1,0), whilst in some taxa this tooth is apparently enlarged to form a protuberance that extends back almost to the propodeal spiracle (1,1).
- 22·1, 22·2 *Propodeal anterior area*. The anterior part of the propodeum (Fig. 50), immediately behind the metanotum, is, in ichneumonids, characteristically depressed to form a transverse groove which is often somewhat broadened medially behind the postscutellum. This presumably plesiomorphic state is found widely in Ophioninae and in virtually all members of the out-groups. Two modifications from this pattern have been observed. In some species the groove is broadened (lengthened) and striate, and thus forms a broad shallow concavity, almost as if the insect had been stretched (Fig. 51) (1,0). The other adaptation is for the groove to be much deeper and present as a U-shaped furrow (Fig. 52) (0,1).
- 23 *Propodeal spiracle*. In the majority of ophionines and members of the out-groups the propodeal spiracle is oval or even subcircular, with the longest axis 4 or less times as long as the shortest. A few ophionines have very large, very elongate spiracles which are 8 or more times as long as broad. This is considered to be an apomorphic development.
- 24·1, 24·2 *Anterior transverse carina of the propodeum*. The presence of this carina, like the other propodeal carinae, is a plesiomorphic feature of ichneumonids as they are complete in fossils (Townes, 1973b). The reduction of this carina is a progressive feature and has been coded as follows – complete (0,0), present only centrally (1,0), absent (1,1).
- 25·1, 25·2 *Posterior transverse carina of the propodeum*. Coded as for character 24 for the same reasons.
- 26 *Longitudinal propodeal impression*. The plesiomorphic condition for ichneumonids is to have the dorsum of the propodeum more or less flat. In a few ophionines a deep longitudinal impression is present and this is considered to be an apomorphic feature.
- 27·1, 27·2, 27·3 *Posterior transverse carina of the mesosternum*. This carina is usually complete in campoplegines and cremastines and thus a complete carina is here considered plesiomorphic for the Ophioninae. The carina is usually lost at two points on either side of the midline, before the mid coxae, so that central and lateral vestiges remain (1,0,0). Sometimes the central vestige is completely lost so only lateral traces remain (1,1,0). In a few species reduction seems to have occurred by loss of only the central part so two broad lateral portions remain (0,0,1).
- 28·1, 28·2 *Lateromedian longitudinal carina of the propodeum*. Coded as for character 24 for the same reasons.
- 29·1, 29·2 *The thyridium*. This is a moderately large indentation found on the second gastral tergite. In its plesiomorphic condition it is close to the anterior margin of the tergite (0,0), but in a number of ophionines it can be seen to have been displaced posteriorly, leaving a scar between itself and the tergal margin (0,1). In a few taxa the thyridium is absent (1,0).
- 30 *Epipleuron of tergite 2*. This is a difficult feature to determine the polarity of as within the out-groups both conditions occur widely. In most ophionines it is upturned, and in a few otherwise specialized taxa it is pendant. The latter condition is tentatively considered to be apomorphic.
- 31 *Profile of tergite 2*. Tergite 2 is laterally compressed in ophionines and members of the closer out-groups (Fig. 2). In profile it is much longer than posteriorly deep. In a few ophionines it is quadrate and this is considered to be an apomorphic development.
- 32 *Position of spiracles on tergite 1*. The plesiomorphic condition for ophionines and members of the out-groups is for the spiracles to be at or behind the level of the margin of the sternite. In a few taxa the spiracles are situated before the sternite margin, a presumed apomorphic condition (1).
- 33 *Presence of an umbo on tergite 2*. The umbo is a convex area on the midline at the anterior margin of tergite 2. It is typically present in many ophionines and members of the out-groups. The apomorphic state (1) is where this structure has been lost.
- 34 *Ovipositor length*. The length of the ovipositor varies a great deal between ichneumonid taxa. Probably the ancestral condition for the family was long, but almost every evolutionary lineage shows reduction. Virtually all ophionines have short straight ovipositors resembling those of many campoplegines (Townes, 1970), and thus this condition is considered to be plesiomorphic. The long ovipositors found in a few taxa are considered to be apomorphic features (1).
- 35 *Ovipositor sheath*. The ovipositor sheaths (valvulae 3) of ichneumonids are almost always slender, just wide enough to enclose the ovipositor. In a few ophionines the sheaths are very stout. This is considered to be an apomorphic development (1).
- 36·1, 36·2, 36·3 *Position of $1m-cu$ in relation to Cu_{1a} in the fore wing*. In most ichneumonids these two veins are quite widely separated and are often at least as far apart as 0·75 of the length of Cu_{1b} . With some reservation this is considered to be the plesiomorphic state (0,0,0). In many ophionines these veins are

separated by about 0.5 times the length of Cu_{1b} (1,0,0), in a number of species by about 0.25 times (1,1,0), whilst in a very few instances the veins are practically contiguous (1,1,1).

- 37 *Length of second discal cell.* The plesiomorphic condition for ichneumonids generally, including ophionines, is for the length of the second discal cell (measured along Cu_{1a}) to exceed 1.10 times the length of the first subdiscal cell (measured along Cu_1). In a number of ophionines the second discal cell is unusually short, being less than the length of the first subdiscal cell. This is considered to be an apomorphic feature (1).
- 38 *Presence of a ramellus.* The ramellus on $1m-cu$ in the fore wing is apparently a remnant of the vein that divided the first discal from the submarginal cell (the two are confluent in all extant ichneumonids though present in fossil forms (Townes, 1973b)). The retention of this stub is tentatively considered to be a plesiomorphic feature, but I have some doubts about the polarity assignment for similar reasons to those stated in 47.1 below.
- 39 *Base of $Rs+2r$ in fore wing.* In the majority of ophionines and members of the out-groups this vein is emitted from the pterostigma at about 30° to the fore margin of the wing; the base of the vein is straight (Fig. 3). In some ophionines the angle of emission is greater ($40^\circ+$) and the vein is rather sharply bent basally (Fig. 4). This is considered to be an apomorphic feature (1).
- 40 *Shaft of $Rs+2r$ in fore wing.* The plesiomorphic condition for Hymenoptera generally is for this vein to be centrally straight; this condition is found widely in out-groups and many ophionines (Fig. 3). In some ophionines the vein is markedly sinuous just before the centre and this (Fig. 6) is considered to be an apomorphic development (1).
- 41 *Position of confluence of Rs and R_1 in fore wing.* In virtually all ophionines and many members of the out-groups these veins meet at the extreme distal apex of the wing so the marginal cell is very long. In a few ophionines the confluence of these veins is more proximal on the fore margin of the wing, away from the tip, so the marginal cell is correspondingly shorter (Fig. 4). This is considered to be an apomorphic feature (1).
- 42.1, 42.2 *Shape of pterostigma.* In most ichneumonids the pterostigma is quite broadly triangular and this plesiomorphic condition prevails in most species in the out-groups. In some ophionines the pterostigma is still broad (0,0) but in many it is not abruptly narrowed distally but evenly tapered (1,0) (Figs 4, 6). In a few the pterostigma is much more slender and elongately tapered (1,1) (Fig. 5).
- 43.1, 43.2 *Position of distal abscissa of Cu_1 in hind wing.* It is very difficult to assign polarity to this character as all stages from Cu_1 close to M to Cu_1 close to $1A$ can be found in members of the out-groups. Furthermore, in most Campopleginae this vein is lost. However, in some of the more primitive ichneumonids the usual condition is for this vein to be closer to M than to $1A$. This is tentatively assumed to be the plesiomorphic condition (0,0). The derived states, treated as a transformation series are: intermediate between M and $1A$ (1,0) and closer to $1A$ than to M (1,1).
- 44.1, 44.2 *Shape of Rs in hind wing.* The plesiomorphic condition of this vein in ichneumonids generally, including many ophionines, is for it to be straight (0,0). In many ophionines it is quite distinctly



Figs 3-6 Fore wings: 3, *Ophion*; 4, *Simophion*; 5, *Stauropectonus*; 6, *Enicospilus*.

- concave whilst in a few taxa it is exceptionally curved so that the distal portion is parallel to the fore margin of the wing. These two derivations are treated as a transformation series and coded 1,0 and 1,1 respectively.
- 45·1, 45·2 *Glabrous area in fore wing.* All primitive ichneumonids, most taxa in the out-groups, and virtually all lower Hymenoptera have the membrane of the fore wing uniformly hirsute close to vein R_s+2r . This is treated as the plesiomorphic condition (0,0). In most ophionines a small glabrous area is present in the discosubmarginal cell near where the pterostigma emits R_s+2r . This is considered apomorphic (1,0). A further specialization is for this area to be very extensive, reaching at least 0·3 of the way along R_s+2r (1,1).
- 46 *Alar sclerites.* The possession of alar sclerites is an unusual apomorphic feature of certain ophionines. Other than in this subfamily these sclerites are only found in two species of ichneumonid (and then in different positions). Elsewhere in the Hymenoptera alar sclerites are apparently only found in some pepsine pompilids (M. C. Day, pers. comm.).
- 47·1, 47·2 *Shape of $1m-cu$ in fore wing.* In the lower Hymenoptera this vein (which in fact is almost certainly not just $1m-cu$ but a composite of this and other vein parts) is angled centrally so the antero-proximal side of the 2nd discal cell is angulate at about 90° . In many ophionines this angulation is present (Fig. 3) and often accompanied by a ramellus (see character 38). This is here tentatively considered to be the plesiomorphic condition (0,0). In many species this vein is evenly curved (1,0), whilst in some it is further modified by being sinuous (1,1). I have certain reservations about the polarity of 47·1 as the evenly curved condition is the widespread condition amongst the out-groups.
- 48·1, 48·2 *Length of $3r-m$ in the fore wing.* In the majority of more primitive ichneumonids $3r-m$ is longer than the abscissa of M between $2m-cu$ and $3r-m$. In many ophionines this is also the case and it is here considered to be the plesiomorphic state (0,0). In some ophionines $3r-m$ is shorter, 0·75–0·50 times as long as M (1,0), whilst in a very few it is extremely reduced, 0·35 or less times the length of M (1,1).
- 49 *Position of abscissa of Cu_1 between $1m-cu$ and Cu_{1a} .* This vein is positioned at about 90° to the axis of the fore wing in most ichneumonids and virtually all lower Hymenoptera. In some ophionines it is specialized in being turned so that it is almost parallel to the wing axis (1).
- 50 *Position of $cu-a$ in fore wing.* The plesiomorphic condition of this vein in ichneumonids is for it to subtend an angle of about 90° to Cu_1 . In a few ophionines it is strongly oblique, subtending an angle of $50-60^\circ$ (1).
- 51·1, 51·2 *Flange on fore tibial spur.* The plesiomorphic state for ichneumonids is the possession of a membranous flange on almost the entire length of the fore tibial spur, immediately behind the microtrichial 'comb' (Fig. 48) (0,0). In some ophionines this is reduced to about 0·3 of the length of the spur (1,0), whilst in others it is entirely lost (Fig. 49) (1,1).
- 52·1, 52·2 *Form of hind trochanter.* The possession of a simple margin to the trochanter is plesiomorphic for ichneumonids (0,0). In a few ophionines a small marginal tubercle is present (1,0), whilst in some cases this may be long, curved and pointed (1,1).
- 53 *Dorsal margin of hind trochanter.* This is also unspecialized in most ichneumonids, but some ophionines are unusual in having a specialization – the margin extended as a flange over the articulation of the trochantellus (1).
- 54 *Hind tibial spurs.* In many ophionines and members of the out-groups these spurs are flattened internally and bear a long fringe of close hairs. In some ophionines they are specialized in being cylindrical and bearing only scattered hairs (1).
- 55 *Penultimate distal hamulus.* The unspecialized condition in Hymenoptera is for the hamuli to be of similar size and shape. In some ophionines the penultimate hamulus is specialized in being very much longer and more coiled than its fellows (1).
- 56 *Grouping of distal hamuli.* The plesiomorphic condition for Hymenoptera is for the row of hamuli to be fairly evenly spaced. In a few ophionines they are arranged in two groups, an apparently specialized condition (1).
- 57 *Number of hamuli distally.* Most primitive Hymenoptera have from 9 to about 15 distal hamuli and, as this condition is widespread in primitive ichneumonids and many ophionines, it is considered plesiomorphic in context of this study. Some ophionines have only 4 or 5 distal hamuli and this reduction is considered to be an apomorphic condition (1).
- 58·1, 58·2 *Shape of hind tarsal claw.* In most members of the out-groups and many primitive ichneumonids the tarsal claws are fairly evenly curved (Fig. 45) and this condition, where it occurs in ophionines is considered to be plesiomorphic (0,0). In Ophioninae the claw may be modified in one of two ways – either by being longer and straighter (1,0) or by being almost geniculate (0,1).
- 59 *Colour of interocellar area.* In most Hymenoptera this area is concolorous with the vertex. In a few

ophionines it is sharply chromatically contrasted, and this is tentatively considered an apomorphic feature (1).

- 60 *Distal pectinal tooth of hind tarsal claw.* The claws of ophionines possess a sinuous row of pectinal teeth or pectinae (Gauld & Mitchell, 1978) forming a comb-like internal surface. This is apparently an apomorphy of the subfamily, so in the present context such a claw may be considered a plesiomorphy. In some ophionines the claw is specialized in having the distal pectinal tooth on the outer surface of the main tooth (Fig. 46) (1).
- 61.1, 61.2 *Taper of mandibular teeth.* In most primitive ichneumonids the mandible is weakly tapered so that the distal apex is more than 0.5 times as broad as the base. This is considered to be the plesiomorphic condition where it occurs in ophionines (0,0). Some species have the mandible more strongly tapered so the apex is 0.4–0.5 times as wide as the base (1,0) whilst a few are exceptional in having the apex <0.3 times as wide as the base (1,1).
- 62 *Thickness of base of Rs+2r.* The plesiomorphic condition for Ichneumonidae is for this vein to be slender at its junction with the pterostigma. In some ophionines it is specialized in being broadened so that close to the pterostigma it is more than twice its central thickness (1).
- 63 *Presence of laterotergite 1 of gaster.* In primitive ichneumonids a distinct laterotergite is present associated with tergite 1; vestiges of this may be found by partial dissection in many ophionines. Some are specialized in having lost this structure (1).
- 64 *Presence of a pectinal comb on both sides of male claw.* The plesiomorphic condition for ophionines is for a single sinuous pectinal comb to be present on the tarsal claws; some males are specialized in having this comb present as a double row of teeth, surrounding a flattened central area (1) (Fig. 47).

Preliminary remarks on the relative values of the characters

For analytical purposes all characters have been treated initially as having equal numerical weight. However, a practising taxonomist does not value characters equally. Intuitively he is more likely to consider some to be more important than others. 'Good' characters are likely to include many of the more bizarre morphological adaptations (Gauld & Mound, 1982). At the other extreme, characters may be considered to have very little value as indicators of phylogenetic affinity. This is often for one of three reasons.

(a) The apomorphic state of the character may involve the disappearance of a structure and, as it is obvious that certain structures are frequently lost in parallel in many distantly related lineages (e.g. the occipital carina has been lost in some taxa independently in virtually all ichneumonid subfamilies), one suspects that an absence in two closely related taxa could also be the result of parallel reduction.

(b) There may be some doubt concerning polarity. This is particularly true in cases where one postulates that a particular state is an apomorphy for the subfamily, but advocates reversal in a few exceptional taxa (e.g. character 12, ocellar size).

(c) Even if the apomorphic condition involves the development of a particular structure, the character may be judged to be unstable, as examination of out-groups suggests it has been derived independently in numerous evolutionary lineages, or is correlated with a particular size range or extreme habitat occupied by a particular species. For example, very large ichneumonids often have similarly coarse reticulate propodeal sculpture, whilst eremic species have short, stout antennae.

The third of these reservations is discussed for individual characters in a subsequent section, but it is appropriate to mention a and b here. Those of the characters used in this study which involve an apomorphic 'loss' are listed below with an asterisk(*), whilst those in which the polarity assignment is suspect are denoted by a prime mark('). This convention is used extensively in the cladograms presented in the following sections. For comparative purposes a list is given below.

1.1*, 1.2*, 2, 3, 4.1, 4.2*, 5.1, 5.2, 6.1, 6.2, 7.1', 7.2', 8.1*, 8.2*, 9, 10, 11, 12*, 13, 14.1', 14.2', 15.1, 15.2, 16.1*', 16.2*', 17, 18.1, 18.2, 19*, 20.1, 20.2, 21.1, 21.2, 22.1, 22.2, 23, 24.1*, 24.2*, 25.1*, 25.2*, 26, 27.1*, 27.2*, 27.3*, 28.1*, 28.2*, 29.1, 29.2*, 30', 31, 32, 33*, 34', 35, 36.1', 36.2', 36.3, 37, 38*', 39, 40, 41, 42.1, 42.2, 43.1', 43.2', 44.1, 44.2, 45.1, 45.2, 46, 47.1', 47.2,

showed only a single discordant state. In the case of 28.1 and 49 the majority state was the derived condition, whilst in the remainder it was the plesiomorphic condition that predominated. As a minimum of two discordant character-states is logically required for a failure, it follows none of these eight can fail; they are shown as 0 --.

The remaining 89 characters have two or more discordant states and therefore can potentially fail the test. Each character was paired with every other one (except for the alternatives *n*. 1 with *n*. 2) and of the 7,855 comparisons made 2,598 resulted in failures. A total of 3,007 failures was expected, so although slightly better than random (O/E value = 0.86), the results suggest a very high incidence of homoplasy. For individual characters a considerable variation in O/E ratio was observed. Characters 6.2, 8.1, 16.1, 21.2, 25.1, 27.3 and 64 all scored better than 0.55, whilst at the other extreme eight characters, 4.2, 10, 36.1, 41, 44.1, 44.2, 50 and 56 all scored worse than 1.00.

Examination of the labels matrix (Appendix 4) showed that two taxa, 909 and 922, had been labelled exceptionally frequently (scoring 89 and 85 labels respectively). Six further species, 906, 908, 921, 923, 942 and 951, were labelled between 45 and 67 times, whilst the rest were labelled less than 42 times. Sixteen taxa were labelled less than ten times and three, 912, 913 and 933 were not labelled at all.

As would be expected, the elimination of bad characters (i.e. those with an exceptionally high O/E score) produced, in general, a progressive improvement in the O/E ratios of the surviving characters. However, the average ratio improved very slowly. With 20 informative characters remaining it was still 0.34. This clearly shows that not all the failures of the 'better' characters were due to clashes with the worst characters; the majority of characters seem to be somewhat homoplastic! Complete elimination of homoplasy (as advocated by LeQuesne, 1972) results in the removal of virtually all characters. The largest cliques contain only ten compatible characters. Several of these have only a very low information value (i.e. have only two or three derived states), but five more informative characters (2, 6.2, 15.1, 15.2 and 22.2) were found to be universal to all the larger cliques. All of these are features that have been used previously in ichneumonid higher classification (Cushman, 1947; Townes, 1971). These characters support the cladogram shown in Fig. 7. Only the group supported by character 2 corresponds with any previously recognized grouping of taxa, the *Thyreodon* group of Cushman (1947).

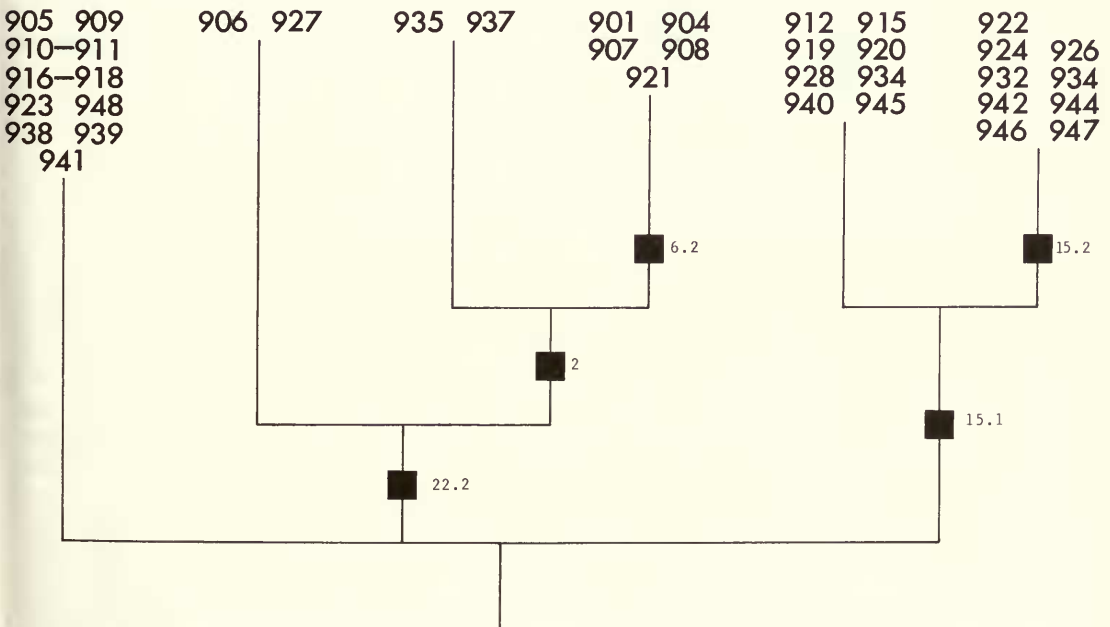


Fig. 7 Cladogram supported by largest clique of compatible characters.

The rate at which the O/E values of individual characters improved (after removal of bad characters) varied tremendously. For example, after removal of the eight worst characters (Table 7), character 29.1, initially the seventy-eighth placed (and the twelfth one scheduled for elimination) progressively improved (with the elimination of each worse character) to sixty-seventh. Character 59, initially placed as sixty-sixth, steadily worsened its position to eighty-third; it would in fact be the tenth character eliminated. If the ten worst characters were removed *en bloc* they would have been 4.2, 10, 36.1, 50, 56, 44.2, 41, 44.1, 31 and 16.2. By stepwise removal of the worst character they would be 4.2, 10, 50, 36.1, 44.1, 41, 39 and 59. All further 'cleaning-up' of data was done by stepwise removal of characters.

Table 7 Results of a LeQuesne test on the primary data matrix after the progressive removal of the highest scoring characters (4.2, 10, 50, 36.1, 44.2, 56, 44.1, 41). Conventions follow table 2; non-informative characters omitted.

| Character number: | | | | incompatibilities observed | | expected | | O/E ratio | | | | | | | |
|-------------------|----|------|------|----------------------------|----|----------|------|---------------|----|------|------|---------------|----|------|------|
| <u>1.1</u> : | 63 | 67.7 | 0.93 | <u>1.2</u> : | 49 | 53.8 | 0.91 | <u>2</u> : | 38 | 68.4 | 0.56 | <u>3</u> : | 40 | 66.7 | 0.60 |
| <u>4.1</u> : | 47 | 54.4 | 0.86 | <u>5.1</u> : | 58 | 71.1 | 0.82 | <u>5.2</u> : | 43 | 57.9 | 0.74 | <u>6.1</u> : | 53 | 61.3 | 0.86 |
| <u>6.2</u> : | 26 | 61.3 | 0.42 | <u>7.1</u> : | 57 | 69.9 | 0.82 | <u>7.2</u> : | 56 | 74.6 | 0.75 | <u>8.1</u> : | 9 | 26.9 | 0.33 |
| <u>9</u> : | 51 | 62.0 | 0.82 | <u>12</u> : | 62 | 69.8 | 0.89 | <u>13</u> : | 48 | 62.0 | 0.77 | <u>14.1</u> : | 60 | 68.8 | 0.87 |
| <u>14.2</u> : | 59 | 73.8 | 0.80 | <u>15.1</u> : | 66 | 75.0 | 0.88 | <u>15.2</u> : | 56 | 69.9 | 0.80 | <u>16.1</u> : | 20 | 47.9 | 0.42 |
| <u>16.2</u> : | 71 | 72.0 | 0.99 | <u>17</u> : | 61 | 66.7 | 0.91 | <u>18.1</u> : | 65 | 70.0 | 0.93 | <u>18.2</u> : | 62 | 67.4 | 0.92 |
| <u>19</u> : | 59 | 62.0 | 0.95 | <u>20.1</u> : | 70 | 73.8 | 0.95 | <u>20.2</u> : | 63 | 74.4 | 0.85 | <u>21.1</u> : | 49 | 61.8 | 0.79 |
| <u>21.2</u> : | 9 | 26.7 | 0.34 | <u>22.1</u> : | 60 | 74.7 | 0.80 | <u>22.2</u> : | 54 | 70.9 | 0.76 | <u>23</u> : | 51 | 68.4 | 0.75 |
| <u>24.1</u> : | 68 | 74.9 | 0.91 | <u>24.2</u> : | 69 | 74.4 | 0.94 | <u>25.1</u> : | 15 | 26.5 | 0.57 | <u>25.2</u> : | 66 | 70.6 | 0.94 |
| <u>26</u> : | 47 | 54.4 | 0.86 | <u>27.1</u> : | 71 | 74.5 | 0.95 | <u>27.2</u> : | 71 | 73.9 | 0.96 | <u>27.3</u> : | 10 | 25.9 | 0.39 |
| <u>28.2</u> : | 64 | 68.4 | 0.94 | <u>29.1</u> : | 44 | 47.7 | 0.92 | <u>29.2</u> : | 72 | 74.9 | 0.96 | <u>30</u> : | 63 | 70.0 | 0.90 |
| <u>31</u> : | 63 | 64.6 | 0.98 | <u>32</u> : | 61 | 66.7 | 0.91 | <u>33</u> : | 64 | 73.9 | 0.87 | <u>35</u> : | 52 | 68.4 | 0.76 |
| <u>36.2</u> : | 71 | 73.8 | 0.96 | <u>36.3</u> : | 54 | 65.7 | 0.82 | <u>37</u> : | 71 | 75.9 | 0.94 | <u>38</u> : | 52 | 58.7 | 0.89 |
| <u>39</u> : | 72 | 73.4 | 0.98 | <u>40</u> : | 44 | 66.7 | 0.66 | <u>42.1</u> : | 60 | 67.4 | 0.89 | <u>42.2</u> : | 53 | 71.7 | 0.74 |
| <u>43.1</u> : | 66 | 68.8 | 0.96 | <u>43.2</u> : | 72 | 74.9 | 0.96 | <u>45.1</u> : | 63 | 70.9 | 0.89 | <u>45.2</u> : | 60 | 74.7 | 0.80 |
| <u>46</u> : | 53 | 70.9 | 0.75 | <u>47.1</u> : | 43 | 57.9 | 0.74 | <u>47.2</u> : | 69 | 71.8 | 0.96 | <u>48.1</u> : | 67 | 75.0 | 0.89 |
| <u>48.2</u> : | 57 | 67.4 | 0.85 | <u>51.1</u> : | 55 | 63.7 | 0.86 | <u>51.2</u> : | 56 | 68.9 | 0.81 | <u>52.1</u> : | 47 | 66.0 | 0.71 |
| <u>52.2</u> : | 42 | 58.0 | 0.72 | <u>54</u> : | 51 | 69.8 | 0.73 | <u>55</u> : | 31 | 54.4 | 0.57 | <u>57</u> : | 68 | 74.8 | 0.91 |
| <u>58.1</u> : | 60 | 71.5 | 0.84 | <u>58.2</u> : | 26 | 26.5 | 0.98 | <u>59</u> : | 73 | 75.6 | 0.97 | <u>60</u> : | 17 | 26.9 | 0.63 |
| <u>61.1</u> : | 65 | 74.4 | 0.87 | <u>61.2</u> : | 65 | 71.7 | 0.91 | <u>62</u> : | 68 | 74.4 | 0.91 | <u>63</u> : | 68 | 75.7 | 0.90 |
| <u>64</u> : | 4 | 26.9 | 0.15 | | | | | | | | | | | | |

Grand total- 2179 observed, 2613.3 expected. Overall O/E ratio = 0.83

Ranking ratios of scoring characters

| | | | | | | | | | | | | | | | | | | | | |
|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|----|------|-----|
| 64 | 8.1 | 21.2 | 27.3 | 16.1 | 6.2 | 2 | 25.1 | 55 | 3 | 60 | 40 | 52.1 | 52.2 | 54 | 42.2 | 5.2 | 47.1 | 23 | 46 | 7.2 |
| 35 | 22.2 | 13 | 21.1 | 14.2 | 15.2 | 22.1 | 45.2 | 51.2 | 7.1 | 5.1 | 36.3 | 9 | 58.1 | 48.2 | 20.2 | 51.1 | 4.1 | 26 | | |
| 6.1 | 33 | 14.1 | 61.1 | 15.1 | 38 | 12 | 45.1 | 42.1 | 48.1 | 63 | 30 | 61.2 | 24.1 | 57 | 1.2 | 62 | 32 | 17 | 18.2 | |
| 29.1 | 24.1 | 18.1 | 1.1 | 37 | 25.2 | 28.2 | 20.1 | 19 | 27.1 | 43.1 | 47.2 | 43.2 | 27.2 | 29.2 | 36.2 | 59 | 31 | | | |
| 58.2 | 39 | 16.2 | | | | | | | | | | | | | | | | | | |

It is apparent from the generally high O/E values that homoplasy is a common feature in the Ophioninae. Any attempt to produce a character set without homoplasy (a clique) necessitates excluding the great majority of characters, including some of the most informative ones. This is unacceptable for two reasons.

(1) A large amount of information would have to be discarded leaving many unresolvable situations. As $2N_t - 2$ apomorphies are necessary to fully resolve N_t taxa, a minimum of 100 compatible characters would be needed to fully resolve the ophionine data. Consequently, without homoplasy, even the full set of 95 characters is insufficient for full resolution. Excluding autapomorphies for definition of terminal taxa, a minimum of 49 characters is necessary for

resolution, but in the present case it can be seen that even discarding half the characters, the resultant data set would still be extremely homoplastic.

(2) It is important to realize that just because a character is homoplastic and has been derived independently in two (or more) lineages, this does not mean that it is not of phylogenetic value. Such a character can still be a genuine synapomorphy for species in two different groups of taxa, and many minimally homoplastic characters are still highly regarded by traditional taxonomists. For example, Mason (1981) states that one of the major synapomorphies of the Braconidae (the probable sister-group of the Ichneumonidae) is the fusion of the second and third gastral tergites. Approximately six of the 60,000 species of Ichneumonidae also have tergites 2 and 3 fused. This parallelism in a few specialized ichneumonids does not eliminate the character as a useful apomorphy for defining Braconidae in a phylogenetic sense, it merely reduces the value of the character as an infallible means of identifying braconids. If it were possible to consider all species of the two taxa Ichneumonidae and Braconidae, it is likely that the O/E value of this character would be very low, but if the analysis were of all Parasitica, and a few taxa from each family were selected as examples of the range of morphological variation, it is quite possible that one of the six anomalous ichneumonids would be included, giving the character a much larger O/E value, and consequently risking its exclusion. In the present study certain species of *Enicospilus*, *Leptophion* and *Laticoleus* were deliberately selected to show the range of morphological variation in the genus, so it is highly likely that these will contribute to the high level of homoplasy in the way outlined above.

In the LeQuesne analysis eight characters were eliminated stepwise until none of the remainder scored worse than 1.00. The particularly high O/E value of these characters strongly suggests they are particularly homoplastic, and consequently of no real value in phylogenetic reconstruction. Considered from a biological point of view it certainly seems these features are homoplastic, but even so several seem to be of use in defining possible holophyletic groups. Considered in order of 'worst' first these characters are as follows.

*4-2**: *reduction of upper tooth of mandible*. The occurrence of the derived state of this feature is limited in the matrix to three species, *Rhynchophion flamipennis* (908), *Sicophion pleuralis* (922) and *Enicospilus unidens* (946). Amongst the Ophioninae in general, this feature is found in the apomorphic state in a group of Madagascan and southern Indian species of *Enicospilus* (Gauld & Mitchell, 1978; 1981) that seem to be related to *E. unidens*, an apparently unrelated Melanesian species (*E. interruptus* Szépligeti) and in an Indian *Ophion* species. Thus although the character has phylogenetic value in some cases (the definition of the *unidens* group) in others it has none. Presumably the apomorphic condition found in three taxa in the matrix is the result of parallel derivation, a conclusion that is strongly suggested by the very high label values (Appendix 4). Amongst out-groups this character is of similar sporadic occurrence (cf. Townes, 1970), sometimes defining an apparent clade and other times being characteristic of a single species. Structurally it is a simple adaptation for biting through fibrous cocoons and as such it is not surprising that it has apparently arisen independently in many different evolutionary lineages.

10: *elongation of maxillae*. This too is a low information value character as the apomorphic condition occurs in just two taxa in the matrix, *Rhynchophion flamipennis* (908) and *Sicophion pleuralis* (922). Amongst other ophionines it is limited in occurrence to some Neotropical species of *Eremotylus*. All of these taxa are restricted to the drier areas of Central and South America and the structural development seems to be an adaptation to drinking from certain flowers. Similar structural modification can be observed in many other ichneumonids in similar habitats, including many Tersilochinae, Cremastinae and Anomaloninae. In arid areas of south-western Australia species of three closely related cremastine genera, *Trathala*, *Temelucha* and *Pristomerus*, all have identically modified maxillae. Only familiarity with the world cremastine fauna enables one to recognize this as evolutionary convergence rather than considering it indicative of a holophyletic group. These observations strongly suggest that particularly intense selection pressures in a particular area may elicit the development in

parallel, of apparently identical apomorphic features in closely related lineages. This may explain the similarity between the taxa in the matrix.

50: oblique position of cu-a in fore wing. Like the preceding two characters this is of low information content as the derived condition occurs in just two taxa in the matrix, *Lepiscelus distans* (909) and *Barytatocephalus mocsaryi* (927). Amongst other ophionines it is limited to occurring in one or two species of *Ophion*. In the sister-group to the Ophioninae, the Campopleginae, the derived condition apparently is useful for defining some genera (e.g. *Cymodusa*, see Townes, 1970) but the character has little apparent phylogenetic significance in the Ophioninae.

36·1': vein 1m-cu separated from Cu_{1a} by less than 0·75, but more than 0·5 of the length of Cu_{1b}. The majority of taxa have this character present in the presumed derived state. Only *Lepiscelus distans* (909), *Stauropocetus occipitalis* (917), *Riekophion emandibulator* (920), *Ophionopsis nigrocyaneus* (921), *Sicophion pleuralis* (922), *Rictophion nebulifer* (937) and *Enicospilus nephele* (944) are plesiomorphic for this feature. It is not found in the plesiomorphic state in any other *Stauropocetus* species, in most other *Enicospilus* species nor any other *Riekophion* species. If the 0 state were a genuine symplesiomorphic feature of these taxa the 1 state must have been derived in parallel in at least species of *Riekophion*, *Enicospilus* and *Stauropocetus* (assuming they are natural genera) and therefore the 1 state is not synapomorphic for all species so scored. Alternatively, if the 1 state is a genuine synapomorphy for all 'other taxa', the 0 state must represent independent reversals in some taxa. Either way the character is homoplastic. The same argument can be applied even if the polarity is reversed, unless one were to accept the otherwise unsupported clade of 909+917+920+921+922+937+944.

44·2: strongly curved Rs in hind wing. In the matrix the apomorphic state of this character is found in *Simophion calvus* (905), *Lepiscelus distans* (909), *Laticoleus curvatus* (915), *Abanchogastra hawaiiensis* (925), *Leptophion maculipennis* (928), *Euryophion adustus* (936), *Rictophion nebulifer* (937) and *Ophion luteus* (939). Elsewhere in the subfamily all species of *Ophion* (ca 150 species) have *Rs* strongly curved. The genus *Abanchogastra* is monotypic, but only some species of *Leptophion*, *Enicospilus*, *Euryophion* and *Laticoleus* possess the apomorphic state as do some species of *Eremotylus* and *Ophiogastrella*. In both *Leptophion* and *Laticoleus* this feature seems to define holophyletic species-groups, but there is no evidence to support the idea that it could be a synapomorphy of all the taxa listed above. Clearly it must have been derived independently in many ophionine lineages, but although a homoplastic feature, it is interesting to note that it still is quite characteristic of certain species-groups and even genera, suggesting that once the apomorphic state has been derived, it is unlikely to undergo reversal.

56: separation of hamuli into two groups. This feature occurs in the matrix only in two Afrotropical species, *Lepiscelus distans* (909) and *Laticoleus curvatus* (915). The latter is the only species in its genus with this particular modification and *Lepiscelus* is monobasic (Gauld & Mitchell, 1978). The apomorphic condition is also found in some central Asian *Ophion* species. The only feature these taxa seem to have in common is that they inhabit rather dry areas. The character appears to have little phylogenetic value.

41: fore wing with R₁ not reaching to tip. The apomorphic condition is found in *Thyreodon atricolor* (901), *Simophion calvus* (905), *Orientospilus melasma* (906), *Ophionopsis nigrocyaneus* (921) and *Sicophion pleuralis* (922). It is not present in many other *Thyreodon* species so it is unlikely that the derived condition in 901 is synapomorphic with that of other species. The exclusion of 901 from the analysis actually resulted in a worsening of the O/E value of this character from 1·02 to 1·12, suggesting it is homoplastic in other taxa. The apomorphic state of this character is found in all species of the genera *Simophion*, *Orientospilus* and *Ophionopsis*, suggesting this feature, once derived, is not likely to undergo reversal.

44·1: bowed vein Rs in hind wing. The apomorphic state of this character is found in all taxa listed under 44·2 above and additionally in 14 other taxa, all from different genera. Elsewhere the feature is of sporadic occurrence in *Ophiogastrella*, *Aulophion*, *Leptophion*, *Laticoleus* and

Enicospilus, as well as being present in all species of *Dictyonotus*, *Hellwigiella*, *Sclerophion*, *Eremotylus*, *Xylophion* and *Rhopalophion*. This suggests parallel development in many different evolutionary lines.

The high O/E values of several of these characters were surprising as almost all represent structural specializations (not 'loss' apomorphies or dubious polarity assignments). Several (4·2, 41 and 44·2) do apparently have considerable phylogenetic value at certain hierarchical levels and really only two (36·1 and 44·1) are likely to be considered by a traditional taxonomist as category 3 'bad' characters. Character 10 almost certainly would intuitively be regarded as a 'good' character (vide Cushman, 1947). It is interesting to note that two taxa (909 and 922) were cited for at least half of the eight worst characters, as having contributed to the high level of homoplasy. These taxa, also recognizable by their high label scores, were subsequently shown to be amongst the more difficult to place, and small differences in their position in the order of taxa submitted to the WAGNER program, produced large changes in the resulting cladogram.

Another estimate of incidences of homoplasy in the primary data may be obtained from perusal of the labels matrix (Appendix 4). Notably high scores, indicative of homoplastic derivation of the apomorphic state in two or more taxa, can be observed for character 1·2 (taxa 909, 923 and 949), 4·1 (906, 909), 4·2 (908, 922, 946), 10 (908, 922), 26 (906, 923), 29·1 (922, 937), 50 (909, 927), 56 (909, 915), 58·2 (942, 951) and 60 (928, 942). The shared plesiomorphic condition for character 38 in taxa 941 and 943 was also highly labelled, suggesting one or other has undergone reversal. Of these 11 characters, six (4·2, 10, 50, 56, 58·2 and 60) are highly labelled for all apomorphic states (two or three in each case), suggesting these are not useful characters for phylogenetic reconstruction. Rather surprisingly all are 'gain' apomorphies. Four (4·2, 10, 50 and 56) are amongst the eight characters eliminated in cleaning up the LeQuesne matrix; one other (58·2) has a higher than average O/E score, but surprisingly one (60) has a reasonably low O/E value.

Analysis using FOURS program

Using the FOURS program a shared derived character matrix (Appendix 3) was computed. This shows the number of derived characters common to each pair of taxa and has values in the range of 3–37. Multiple linkage clusters drawn for taxa with 29+ shared derived characters are shown in Fig. 8. Four groups are apparent. The largest includes 17 species (912–5, 919, 924, 928–30, 932–4, 942–3, 945–7), the last eight of which form a particularly closely knit group. Taxon 925 and the reciprocal nearest neighbours 911 and 910 are less strongly associated with this group. This complex contains most of the species of *Enicospilus* and *Leptophion*, all *Dicamptus*, *Laticoleus* and *Pamophion*, together with *Ophiogastrella* and representatives of two of the three endemic Hawaiian genera, *Pycnophion* and *Abanchogastra*. It is noteworthy that *Enicospilus nephele* (944) and *Leptophion tetus* (931) are not associated. Each of these taxa share less derived characters with their supposed congeners than their congeners share with other taxa, although in each case the species' nearest neighbours are its congeners (Table 13).

Taxa 916, 917 and 918 (the *Stauropoctonus* group) form a cluster with 30–34 derived characters in common. This group seems to be associated with the *Enicospilus* group quite closely as 918 shares 28 derived characters with 947, 943, 942 and 919.

Taxa 935, 936 and 937 (the *Euryophion* group) cluster with 30–32 shared derived characters.

Taxa 901–4 (the *Thyreodon* group) form a cluster sharing 28–32 derived characters. Also associated with this cluster are the reciprocal nearest neighbours 907 and 921 (*Dictyonotus/Ophionopsis*).

When linkages of more than 22 shared derived characters are considered (Fig. 9), the majority serve to consolidate the clusters already formed. The *Stauropoctonus* group and *Ophiogastrella* are repeatedly linked to the *Enicospilus* cluster (both having in excess of 60% of possible linkages to the latter) as does taxon 931. Taxa 926 and 944 are less strongly but uniquely associated with this group and taxon 949 also links to this group. The *Thyreodon*, *Euryophion* and *Dictyonotus/Ophionopsis* groups, together with taxon 908, form a second robust cluster with only *Euryophion* showing any linkage to non-group taxa. Taxon 909 is somewhat

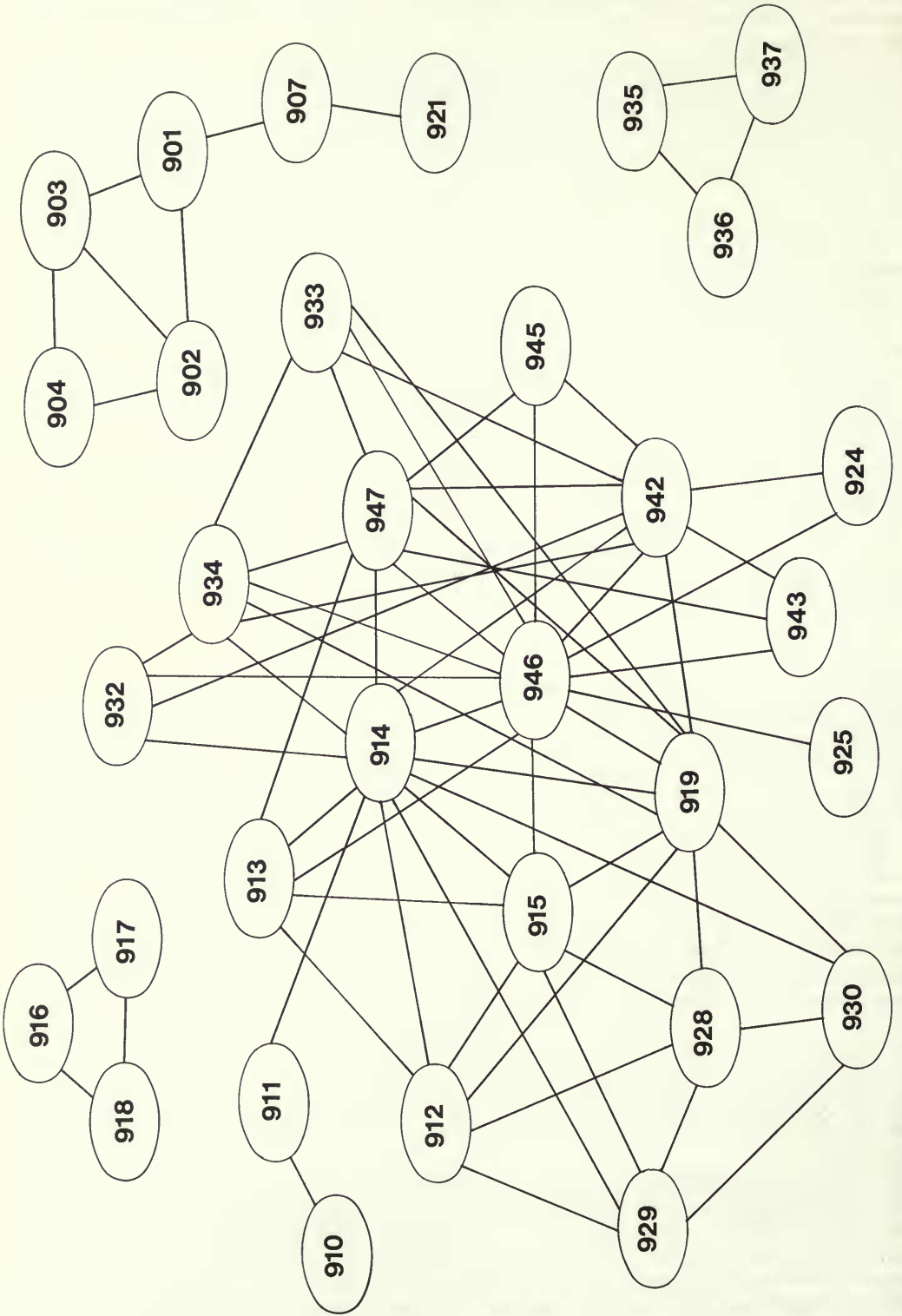


Fig. 8 Multiple linkage clusters drawn for all taxa with 29 or more derived characters in common.

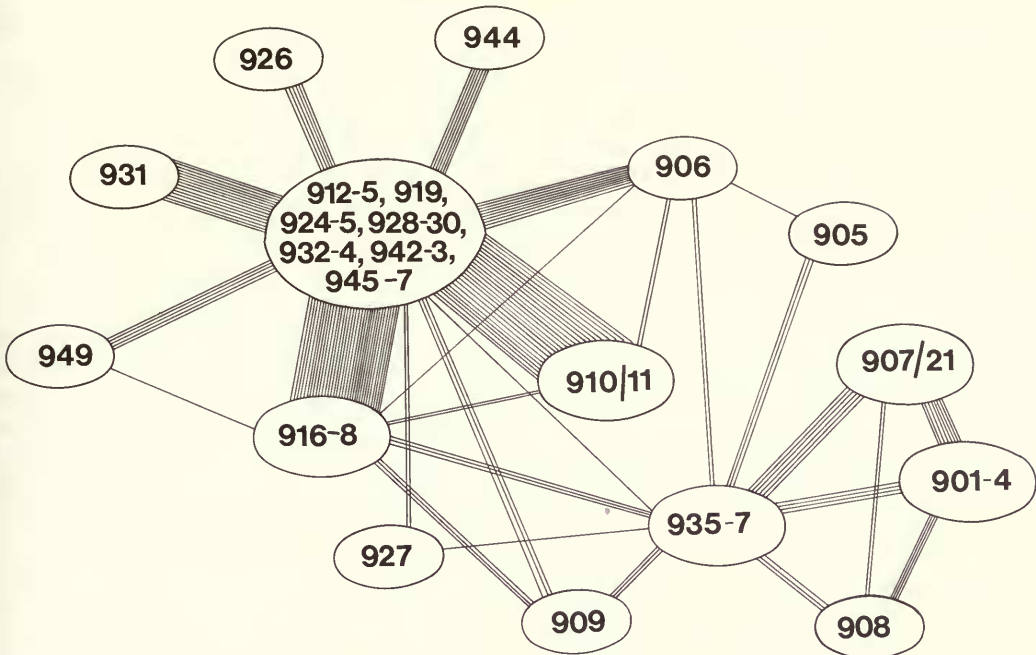


Fig. 9 Multiple linkage clusters drawn for all taxa with 22 or more derived characters in common. As virtually complete linkages occur between taxa enclosed within the boxes, these linkages are not shown so as to avoid confusion.

intermediate linking to both the *Enicospilus* and *Euryophion* groups but shares most derived features with taxa in the *Stauropoctonus* group.

Other taxa occupy a more ambivalent position. Taxon 906 is intermediate between *Enicospilus* and *Euryophion*, whilst 905 appears to be fairly closely associated with *Euryophion* although its nearest neighbour is taxon 906. Taxon 927 is also intermediate. The remaining species, 920, 922, 923, 938-41, 948 and 950-51, are not closely associated with other taxa. To summarize therefore, two major groups are discernible, the *Enicospilus/Stauropoctonus* complex containing taxa 909-919, 924-926, 928-934, 942-947 and 949, and the *Thyreodon/Euryophion* complex with taxa 901-904, 907-908, 921 and 935-937. Taxa 920, 922, 923, 938-941, 948 and 950-951 are not associated at all whilst 905, 906 and 927 are intermediates between the major clusters. It is interesting to note that, excluding the last three taxa, the remainder could be classified phenetically (if one counted shared plesiomorphies of which 920, 922, 938-941, 948 and 950-951 have a considerable number in common) into three groups approximately corresponding to the *Ophion* (plesiomorphic group), *Thyreodon* and *Enicospilus* groups of Cushman (1947).

Phylogenetic analyses of groups of ophionine taxa

The Euryophion group (taxa 935, 936, 937)

It can be seen from Appendix 3 that these taxa form a group with 30+ shared derived characters, and no more than 26 derived characters in common with any other taxon. Using these three as the fixed taxa (3F option) of FOURS, and trying them against all other taxa, nothing broke them up. The three taxa were found to share 29 apomorphies (2, 6·1, 7·1, 16·1, 16·2, 22·2, 24·1, 24·2, 25·1, 25·2, 27·1, 28·1, 28·2, 31, 32, 38, 39, 42·1, 42·2, 43·1, 44·1, 45·1, 47·1, 49, 51·1, 51·2, 58·1, 61·1 and 62). Five of these apomorphies (2, 7·1, 22·2, 42·2 and 58·1) have average or lower O/E values (0·60, 0·84, 0·80, 0·79 and 0·87 respectively) and are shared by relatively few other taxa in the matrix. Of these five apomorphies only one (7·1) has questionable polarity. No character is a

unique apomorphy of the group, but the four apomorphies accepted above suggest this group is monophyletic.

There are three possible arrangements of these taxa (Fig. 10). Taxa 935 and 936 have been considered to be congeneric (in *Euryophion*) whilst 937 is usually placed in a separate genus, *Rictophion* (Townes, 1971; Gauld & Mitchell, 1978). *Rictophion* has been separated from *Euryophion* by two unique apomorphies, loss of thyridia and possession of 3-segmented palps. Cladogram A supporting this arrangement is the weakest of the three as it involves only a single informative character, 36.1 which has both a dubious polarity assignment and a very high O/E score. Both B and C also involve some poor scoring characters (19 and 44.2 both have O/E values of more than 0.95). Arrangement B is only supported by 'loss' apomorphies, though one (8.1) has a low O/E value (0.39). However, it has a rather high label score. The characters supporting C are all fairly high scoring (O/E values 0.76+) but do not involve either apomorphic loss or dubious polarity assignment. On balance therefore, C seems to be the preferable arrangement, suggesting that *Euryophion*, as currently recognized, is paraphyletic with respect to *Rictophion*. This conclusion is not surprising as originally *Rictophion* was separated from *Euryophion* on the basis of two autapomorphies. *Rictophion ikuthana* (937), the only species in the genus, can be regarded as a specialized species of *Euryophion*. These species, and all the remainder in the genus, are further analysed below (p. 136).

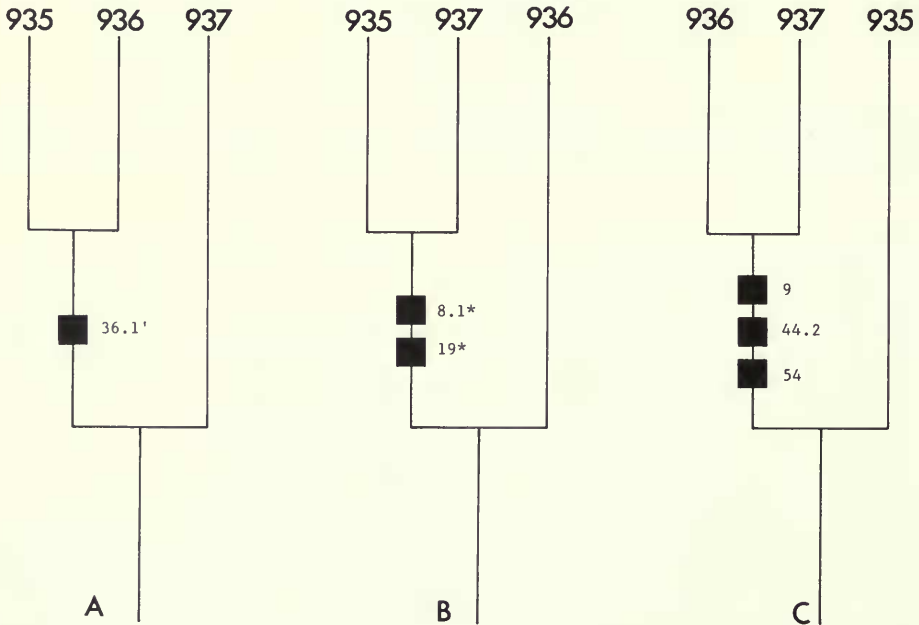


Fig. 10 The three possible dichotomous arrangements of *Euryophion latipennis* (935), *E. adustus* (936) and *Rictophion ikuthana* (937).

The Thyreodon group (taxa 901, 902, 903, 904)

These four taxa, all species currently placed in the genus *Thyreodon* (Townes & Townes, 1966), form a closely knit group. Using the FOURS 3F option any combination of these species remained as a group when tested against any fourth taxon. The *Thyreodon* species share 27 apomorphies (2, 6.2, 7.1, 14.1, 17, 22.2, 23, 24.1, 24.2, 25.1, 25.2, 27.1, 28.1, 28.2, 29.2, 30, 33, 36.1, 38, 42.1, 42.2, 47.1, 49, 51.1, 51.2, 54 and 61.1). Seven of these apomorphies (2, 6.2, 7.1, 22.2, 23, 42.2 and 54) have both lower than average O/E scores (0.60, 0.47, 0.84, 0.80, 0.78, 0.79 and 0.76 respectively) and are shared by relatively few other taxa. Only one, 7.1, involves dubious polarity assignment; the remainder are gain apomorphies suggesting the group is

monophyletic. Considering the possible phylogenetic relationships of these taxa to each other, the following result was obtained using the FOURS program (Underwood, 1982).

| TAXA NOS. - | 901 | 902 | 903 | 904 |
|-------------|-----|-----|-------|---------|
| X | | | 1100: | 12* 13 |
| X' | | | 0011: | 36·2' |
| Y | | | 1010: | 21·1 |
| XYZ' | | | 1110: | 26 58·1 |
| XY'Z | | | 1101: | 37 |
| X'Y'Z' | | | 0111: | 9 |

The most favoured arrangement X,XYZ' is shown in Fig. 11. This involves three forward parallelisms 21·2 (in 901 and 903), 37 (in 901/2 and 904) and 36·2 (in 903 and 904) and one reversal (9 in 901). If the dubious polarity of 36·2 were to be reversed this character would fit the cladogram. It is noteworthy that some authors (e.g. Ashmead, 1900; Cushman, 1947) have placed taxon 904 and its relatives in a separate genus, *Athyreodon*.

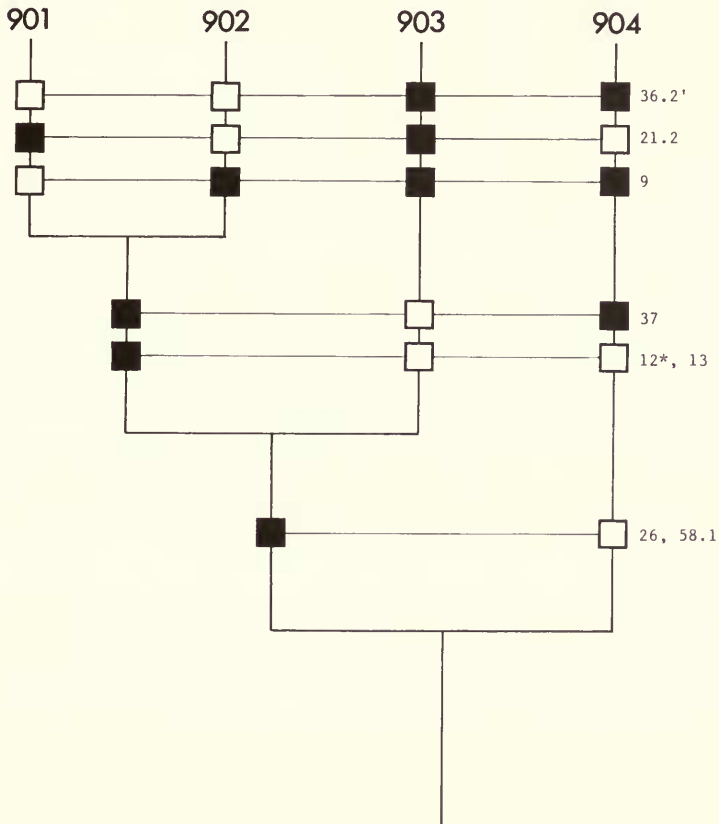


Fig. 11 The arrangement of *Thyreodon* species as supported by the largest number of compatible characters.

The Dictyonotus/Ophionopsis group (taxa 907, 921)

These two taxa are reciprocal nearest neighbours. They share 30 apomorphies (2, 6·2, 7·1, 12, 13, 14·1, 16·2, 18·2, 21·1, 21·2, 22·2, 23, 24·1, 24·2, 25·1, 25·2, 28·1, 28·2, 30, 33, 38, 42·1, 42·2, 44·1, 47·1, 49, 51·1, 51·2, 54 and 58·1). Ten of these (2, 6·2, 7·1, 21·1, 21·2, 22·2, 23, 42·2, 54 and 58·1) have both average or lower O/E values (0·60, 0·47, 0·84, 0·79, 0·39, 0·80, 0·78, 0·79, 0·76 and 0·87 respectively) and are shared by relatively few other taxa in the matrix. One character,

21·2, is a unique apomorphy of this group. The primary label matrix (Appendix 4) suggests characters 16·1, 36·1 and 61·1 (0 scores in taxon 921) may have undergone reversal, whilst character 47·2 (1 score in 921) may have been derived in parallel in 921 and other taxa.

The Thyreodon + Euryophion + Dictyonotus complex (the above three groups)

These three groups of taxa appear to be associated (see shared derived character matrix, Appendix 3). Phylogenetically they also seem to form a distinctive clade, sharing 16 apomorphic features (2, 7·1, 22·2, 24·1, 24·2, 25·1, 25·2, 28·1, 28·2, 38, 42·1, 42·2, 47·1, 49, 51·1 and 51·2). Four of these apomorphies (2, 7·1, 22·2 and 42·2) have both lower than average O/E values (0·60, 0·84, 0·80 and 0·79 respectively) and are shared by very few other taxa. Character 2 is elsewhere only found in the apomorphic state in taxon 908, character 7·1 is apomorphic for taxa 908, 940 and 946, character 22·2 is apomorphic for taxa 906, 908, 927 and 950, whilst character 42·2 is otherwise only apomorphic for taxa 908, 909, 916, 917 and 918. Examination of the labels matrix (Appendix 4) shows that for character 7·1, species 940 and 946 are labelled more than twice as frequently as any other taxon. Similarly for character 22·2, species 906 and 950 are fairly highly labelled. These data suggest parallel derivation of the apomorphic condition of these characters in taxa 906, 940, 946 and 950.

Three other characters are found in the apomorphic condition in all except one taxon in the group. Of these, 61·1 has a high label score for taxon 921, suggesting the apparent plesiomorphic condition in this taxon may be a reversal. Character 54 is present in the apomorphic condition in all taxa in this group except 935; elsewhere it is only found, in the data matrix, in the derived state in three taxa, 908, 941 and 950. The higher values of these last two species suggest the apomorphic state may have been derived in parallel in them. The third of the three characters, 58·1, is usually found in the derived state in *Thyreodon*, so may be presumed to have undergone reversal in 904. Elsewhere it is only found in the apomorphic state in taxa 908, 909, 927, 941 and 950. Taxon 909 has a high label score for this character, suggesting homoplasy. It seems reasonable to treat tentatively all these three characters as apomorphies of the group. This interpretation is certainly the most parsimonious, for in each case the alternative to single postulated reversals must be the advocacy of multiple forward parallelisms.

One other taxon, 908, seems to be consistently associated with this group. Its nearest neighbours all lie within the group (Table 8), and in cluster analysis it readily associated with the group. It shares 18 of the 19 apomorphies of the group and is discordant only in having character

Table 8 The *Thyreodon*/*Euryophion* complex showing nearest neighbours with numbers of shared derived characters. The rows give the five (or more if several are equal fifth) nearest neighbours of each taxon listed in the left-hand column. The columns show the number of times a species is cited as a near neighbour. It can be seen that taxon 908 occupies an intermediate position between *Thyreodon* (901–4) and *Euryophion* (935–7), having nearest neighbours in both. The *Thyreodon* and *Euryophion* groups have only one near neighbour in common (904–936). Only species in the latter group share large numbers of derived characters in common with non-group taxa (the 'others' column). It is interesting to note that taxon 907, the least autapomorphic in this group (see p. 89), is cited as a near neighbour by all other taxa.

| | 901 | 902 | 903 | 904 | 907 | 921 | 908 | 935 | 936 | 937 | Others |
|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|---------------------|
| 901 | + | 32 | 30 | 28 | 30 | 27 | -- | -- | -- | -- | |
| 902 | 32 | + | 30 | 29 | 28 | 26 | -- | -- | -- | -- | |
| 903 | 30 | 30 | + | 29 | 27 | 25 | 25 | -- | -- | -- | |
| 904 | 28 | 29 | 29 | + | 26 | -- | -- | -- | 26 | -- | |
| 907 | 30 | 28 | 27 | -- | + | 30 | 28 | -- | -- | -- | |
| 921 | 27 | 26 | 25 | -- | 30 | + | 27 | -- | -- | -- | |
| 908 | 25 | 25 | 25 | -- | 28 | 27 | + | 25 | 25 | 27 | |
| 935 | -- | -- | -- | -- | 24 | -- | 25 | + | 30 | 31 | (23– 905, 906, 918) |
| 936 | -- | -- | -- | 26 | 26 | -- | -- | 30 | + | 32 | (26– 946) |
| 937 | -- | -- | -- | -- | 24 | 24 | 27 | 31 | 32 | + | (25– 905; 24– 906) |

28.2 plesiomorphic. However, this character is highly labelled for this taxon suggesting a reversal. In FOURS analyses taxon 908 repeatedly broke into the group. For example –

| | | | | | |
|-----------------|-----|-------|------|------|------------|
| TAXA NOS. – 901 | 921 | 936 | 908 | | |
| X | | 1100: | 21.1 | 30 | 41 |
| X' | | 0011: | 16.1 | | |
| Y | | 0101: | 18.2 | | |
| Y' | | 1010: | 29.2 | 37 | |
| Z | | 0110: | 9 | | |
| XYZ' | | 1110: | 13 | 28.2 | |
| XY'Z | | 1101: | 6.2 | 12 | 14.1 23 33 |
| X'YZ | | 1011: | 27.1 | 36.1 | 61.1 |
| X'Y'Z' | | 0111: | 16.2 | 31 | 32 44.1 |

| | | | | | |
|-----------------|-----|-------|------|------|------------|
| TAXA NOS. – 901 | 907 | 936 | 908 | | |
| X | | 1100: | 20.1 | 21.1 | 30 |
| X' | | 0011: | 31 | 32 | |
| Y | | 1010: | 37 | | |
| Y' | | 0101: | 18.2 | | |
| Z | | 0110: | 43.1 | | |
| XYZ' | | 1110: | 13 | 28.2 | 29.2 |
| XY'Z | | 1101: | 6.2 | 12 | 14.1 23 33 |
| X'YZ | | 1011: | 27.1 | | |
| X'Y'Z' | | 0111: | 16.1 | 16.2 | 44.1 |

In both these cases exclusion of taxon 908 from the group, the XYZ' option, is not the most parsimonious solution. Accordingly, taxon 908, *Rhynchophion flammipennis*, is included for analysis in this group.

Considering only the ten taxa of this group, 35 characters are informative for examining intra-group relationships. A LeQuesne test on this subset of data yielded the results shown in Table 9. Progressive removal of the five worst characters (59, 36.1, 27.2, 9 and 39) markedly altered the ranking of the 'best' scoring characters (i.e. those with an O/E value of 0.6+); the overall O/E ratio improved from 0.69 to 0.52 (Table 10). The data matrix was re-ordered with characters arranged in increasing value of O/E ratio (Tables 11, 12) before and after removal of the worst characters. Considering only the characters with an O/E value greater than 0.55 shows that there are two competing patterns. Characters 16.2, 44.1, 31 and 32 unite the *Euryophion* group (935–7) with the *Dictyonotus* group (907, 921) and 908. This arrangement is contradicted by characters 14.1, 23, 33 and 6.2, which all favour uniting the *Dictyonotus* group with

Table 9 Results of a LeQuesne test on the *Thyreodon/Euryophion* data set. Conventions as in Table 2.

| Character number: incompatibilities observed expected O/E ratio | | | | | | | | | | | | | | | | | | | |
|--|------|------|------|---------------|----|------|------|---------------|----|------|------|---------------|------|------|------|------|----|----|------|
| <u>6.1</u> : | 11 | 22.9 | 0.48 | <u>6.2</u> : | 11 | 22.9 | 0.48 | <u>8.1</u> : | 7 | 16.2 | 0.42 | <u>9</u> : | 30 | 26.9 | 1.11 | | | | |
| <u>12</u> : | 18 | 27.9 | 0.65 | <u>13</u> : | 26 | 27.9 | 0.93 | <u>14.1</u> : | 11 | 23.6 | 0.47 | <u>16.1</u> : | 18 | 26.0 | 0.69 | | | | |
| <u>16.2</u> : | 11 | 26.0 | 0.42 | <u>17</u> : | 12 | 26.9 | 0.45 | <u>18.2</u> : | 24 | 26.9 | 0.89 | <u>19</u> : | 17 | 23.6 | 0.72 | | | | |
| <u>20.1</u> : | 11 | 16.2 | 0.68 | <u>21.1</u> : | 18 | 26.4 | 0.68 | <u>21.2</u> : | 9 | 15.6 | 0.58 | <u>23</u> : | 11 | 23.6 | 0.47 | | | | |
| <u>26</u> : | 10 | 23.6 | 0.42 | <u>27.1</u> : | 9 | 15.7 | 0.57 | <u>27.2</u> : | 28 | 23.1 | 1.21 | <u>29.2</u> : | 22 | 26.9 | 0.82 | | | | |
| <u>30</u> : | 20 | 23.6 | 0.85 | <u>31</u> : | 15 | 27.9 | 0.54 | <u>32</u> : | 15 | 27.9 | 0.54 | <u>33</u> : | 11 | 23.6 | 0.47 | | | | |
| <u>36.1</u> : | 21 | 15.7 | 1.34 | <u>36.2</u> : | 23 | 23.1 | 1.00 | <u>37</u> : | 25 | 26.9 | 0.93 | <u>39</u> : | 17 | 26.9 | 0.63 | | | | |
| <u>41</u> : | 14 | 16.2 | 0.87 | <u>43.1</u> : | 19 | 26.9 | 0.71 | <u>44.1</u> : | 12 | 26.4 | 0.45 | <u>44.2</u> : | 9 | 15.6 | 0.58 | | | | |
| <u>45.1</u> : | 11 | 23.6 | 0.47 | <u>59</u> : | 23 | 16.2 | 1.42 | <u>62</u> : | 11 | 23.6 | 0.47 | | | | | | | | |
| Grand total – 280 observed, 406.3 expected. Overall O/E ratio = 0.69 | | | | | | | | | | | | | | | | | | | |
| Ranking ratio of scoring characters | | | | | | | | | | | | | | | | | | | |
| 16.2 | 26 | 8.1 | 17 | 44.1 | 62 | 33 | 45.1 | 14.1 | 23 | 6.1 | 6.2 | 31 | 32 | 27.1 | 21.2 | 44.2 | 39 | 12 | 20.1 |
| 21.1 | 16.1 | 43.1 | 19 | 29.2 | 30 | 41 | 18.2 | 37 | 13 | 36.2 | 9 | 27.2 | 36.1 | 59 | | | | | |

Table 10 Results of a LeQuesne test on the *Thyreodon/Euryophion* data set after progressive removal of five highest scoring characters (59, 36·1, 27·2, 9, 39). Conventions as in Table 2.

| Character number: | | incompatibilities observed | | | expected | | | O/E ratio | | | | | | | | | | | |
|-------------------------------------|------|----------------------------|------|-------|-----------------|------|------|--------------------------|------|------|------|-------|----|------|------|----|------|------|----|
| 6.1: | 6 | 19.6 | 0.31 | 6.2: | 6 | 19.6 | 0.31 | 8.1: | 3 | 13.9 | 0.22 | 12 : | 14 | 24.1 | 0.58 | | | | |
| 13 : | 23 | 24.1 | 0.96 | 14.1: | 6 | 20.3 | 0.30 | 16.1: | 13 | 22.3 | 0.58 | 16.2: | 7 | 22.3 | 0.31 | | | | |
| 17 : | 8 | 23.2 | 0.34 | 18.2: | 22 | 23.2 | 0.95 | 19 : | 13 | 20.3 | 0.64 | 20.1: | 10 | 13.9 | 0.72 | | | | |
| 21.1: | 13 | 22.7 | 0.57 | 21.2: | 7 | 13.4 | 0.52 | 23 : | 6 | 20.3 | 0.30 | 26 : | 6 | 20.3 | 0.30 | | | | |
| 27.1: | 7 | 13.9 | 0.50 | 29.2: | 19 | 23.2 | 0.82 | 30 : | 16 | 20.3 | 0.79 | 31 : | 11 | 24.1 | 0.46 | | | | |
| 32 : | 11 | 24.1 | 0.46 | 33 : | 6 | 20.3 | 0.30 | 36.2: | 20 | 20.3 | 0.98 | 39 : | 12 | 23.2 | 0.52 | | | | |
| 41 : | 11 | 13.9 | 0.79 | 43.1: | 14 | 23.2 | 0.60 | 44.1: | 8 | 22.7 | 0.35 | 44.2: | 6 | 13.4 | 0.45 | | | | |
| 45.1: | 6 | 20.3 | 0.30 | 62 : | 6 | 20.3 | 0.30 | | | | | | | | | | | | |
| Grand total- | | 158 observed, | | | 303.4 expected. | | | Overall O/E ratio = 0.52 | | | | | | | | | | | |
| Ranking ratio of scoring characters | | | | | | | | | | | | | | | | | | | |
| 8.1 | 45.1 | 62 | 23 | 26 | 33 | 14.1 | 6.1 | 6.2 | 16.2 | 17 | 44.1 | 44.2 | 31 | 32 | 27.1 | 39 | 21.2 | 21.1 | 12 |
| 16.1 | 43.1 | 19 | 20.1 | 30 | 41 | 29.2 | 18.2 | 13 | 36.2 | | | | | | | | | | |

Thyreodon (901–4). Characters 6·1, 8·1, 17, 26, 45·1 and 62 clash with neither of these combinations and so, in this context, are uninformative. The very best characters in the original 35 character set (Table 11) favour the former grouping whilst in the ‘cleaned-up’ 30 character set (Table 12) the best characters favour *Thyreodon* + *Dictyonotus*. Of the eight characters in the two contradictory groups, two, 16·2 and 33, are ‘loss’ apomorphies and perhaps therefore the apomorphic state is particularly likely to be subject to parallel development. Even disregarding these one is still left with a tie with three characters supporting each arrangement, so it is necessary to consider further characters. Of the characters having an initial O/E value of average or better (16·2–16·1 in Table 11) two, 12 and 21·1, suggest uniting *Thyreodon* with *Dictyonotus* if one postulates minimal reversal in *Thyreodon*. Character 27·1 suggests uniting *Thyreodon* with *Euryophion* and taxon 908, whilst 21·2 is an autapomorphy of taxa 907 and 921. Character 39 suggests linking a single *Thyreodon* species with *Euryophion*. Character 20·1 is apomorphic in only two taxa, 901 and 907.

Considering all characters the most parsimonious arrangement appears to be to treat *Euryophion* as the first branch. By postulating minimal homoplasy (i.e. single reversals or parallelisms) 12 characters can be made to support this arrangement. Only three, 30, 43·1 and 44·2, have an O/E value below average, and only one, 33, is a ‘loss’ apomorphy. This arrangement involves the following homoplasy (and these are considered to be predictable from the *Thyreodon* labels matrix (Appendix 5) if, for a particular character, the score obtained by the presumed discordant species is higher than that obtained by other species in the group) – 12, reversal in 903/4 (not predictable); 30, reversal in 908, parallelism in 935 (predictable); 39,

Table 11 The *Thyreodon/Euryophion* complex with all 35 informative characters ranked according to their initial O/E value (lowest first). All characters to the left of 27·1 have an O/E value of 0.55 or less.

| | 16.2 | 8.1 | 44.1 | 33 | 14.1 | 6.1 | 31 | 27.1 | 44.2 | 12 | 21.1 | 43.1 | 29.2 | 41 | 37 | 36.2 | 27.2 | 59 | | | | | | | | | | | | | | | | | |
|-----|------|-----|------|------|------|-----|----|------|------|------|------|------|------|------|----|------|------|----|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 26 | 17 | 62 | 45.1 | 23 | 6.2 | 32 | 21.2 | 39 | 20.1 | 16.1 | 19 | 30 | 18.2 | 13 | 9 | 36.1 | | | | | | | | | | | | | | | | | | |
| 901 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | | | | | |
| 902 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | | | |
| 903 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | | |
| 904 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | | |
| 908 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | | |
| 907 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | |
| 921 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | |
| 937 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 |
| 935 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 |
| 936 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 0 |

Table 12 The *Thyreodon/Euryophion* complex with the 30 'best' informative characters ranked by O/E value computed after progressive removal of five highest scoring characters (see Table 10). All characters to the left of 21.1 have an O/E value of 0.55 or less.

| | 8.1 | 6.2 | 26 | 14.1 | 6.2 | 17 | 44.2 | 32 | 39 | 21.1 | 16.1 | 19 | 30 | 29.2 | 13 | | | | | | | | | | | | | | | | | | | | |
|-----|------|-----|----|------|------|------|------|------|------|------|------|------|----|------|------|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 45.1 | 23 | 33 | 6.1 | 16.2 | 44.1 | 31 | 27.1 | 21.2 | 12 | 43.1 | 20.1 | 41 | 18.2 | 36.2 | | | | | | | | | | | | | | | | | | | | |
| 901 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | | | | | | | | |
| 902 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | | | | |
| 903 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | | | |
| 904 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | | |
| 908 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | |
| 907 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | |
| 921 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | |
| 937 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 |
| 935 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 936 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 0 |

parallelism in 904 (predictable); 43.1, parallelism in 907 (predictable); 44.2, parallelism in 921 and reversal in 935 (not predictable).

In attempting to resolve the sister-lineage of *Euryophion*, the *Thyreodon/Dictyonotus/Rhynchophion* branch, it is apparent that no character is a unique apomorphy of either *Rhynchophion* + *Dictyonotus*, *Rhynchophion* + *Thyreodon* or *Dictyonotus* + *Thyreodon*. Character 30 suggesting the latter is paralleled in taxon 935, 16.2 and 44.1 suggesting *Rhynchophion* + *Dictyonotus* are paralleled in *Euryophion* as is character 27.1 which favours uniting *Rhynchophion* + *Thyreodon*. In any compatibility cladogram (e.g. Fig. 12) these three taxa must remain as an unresolved trichotomy.

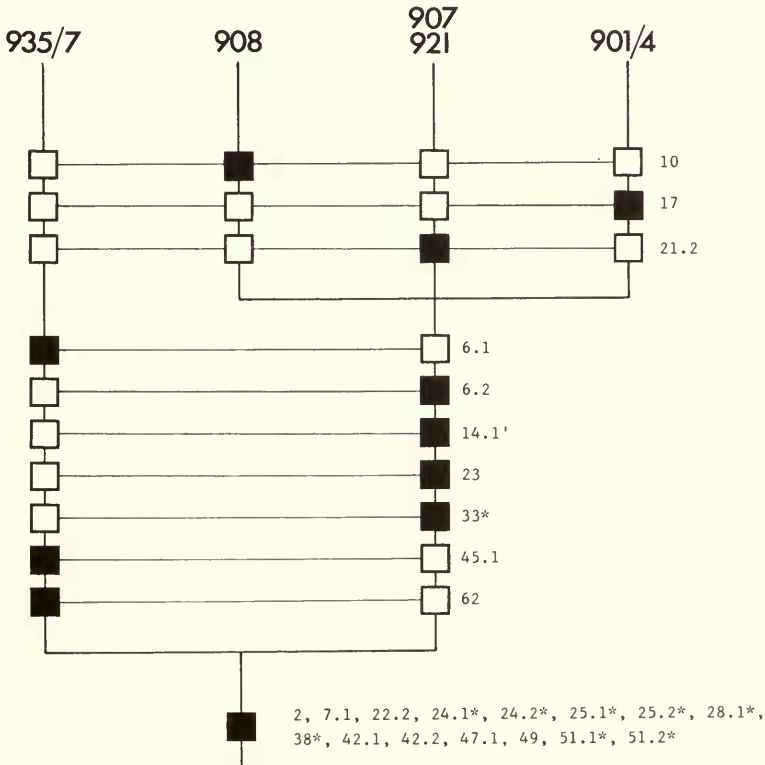


Fig. 12 Cladogram showing inter-relationships of taxa in the *Thyreodon/Euryophion* complex as supported by the largest compatible clique.

To resolve these data further it was necessary to use the WAGNER option of PHYLIP. The shortest rooted tree obtained involved 83 transformation steps for the 45 characters showing both 0 and 1 states for this group of taxa (that is the 35 characters shown in the LeQuesne matrix (Table 11) plus 1·1, 4·2, 8·2, 10, 18·1, 29·1, 36·3, 43·2, 47·2 and 57 which are autapomorphies of various individual taxa). To obtain this tree (Fig. 13) 21 characters (1·1, 4·2, 6·1, 6·2, 8·2, 10, 14·1, 17, 18·1, 21·2, 23, 26, 29·1, 33, 36·3, 43·2, 44·2, 45·1, 47·2, 57 and 62) are presumed to have been uniquely derived, 11 characters (8·1, 12, 16·2, 18·2, 20·1, 27·1, 39, 41, 43·1, 44·1 and 59) have undergone two transformations (i.e. have either been derived in parallel or have

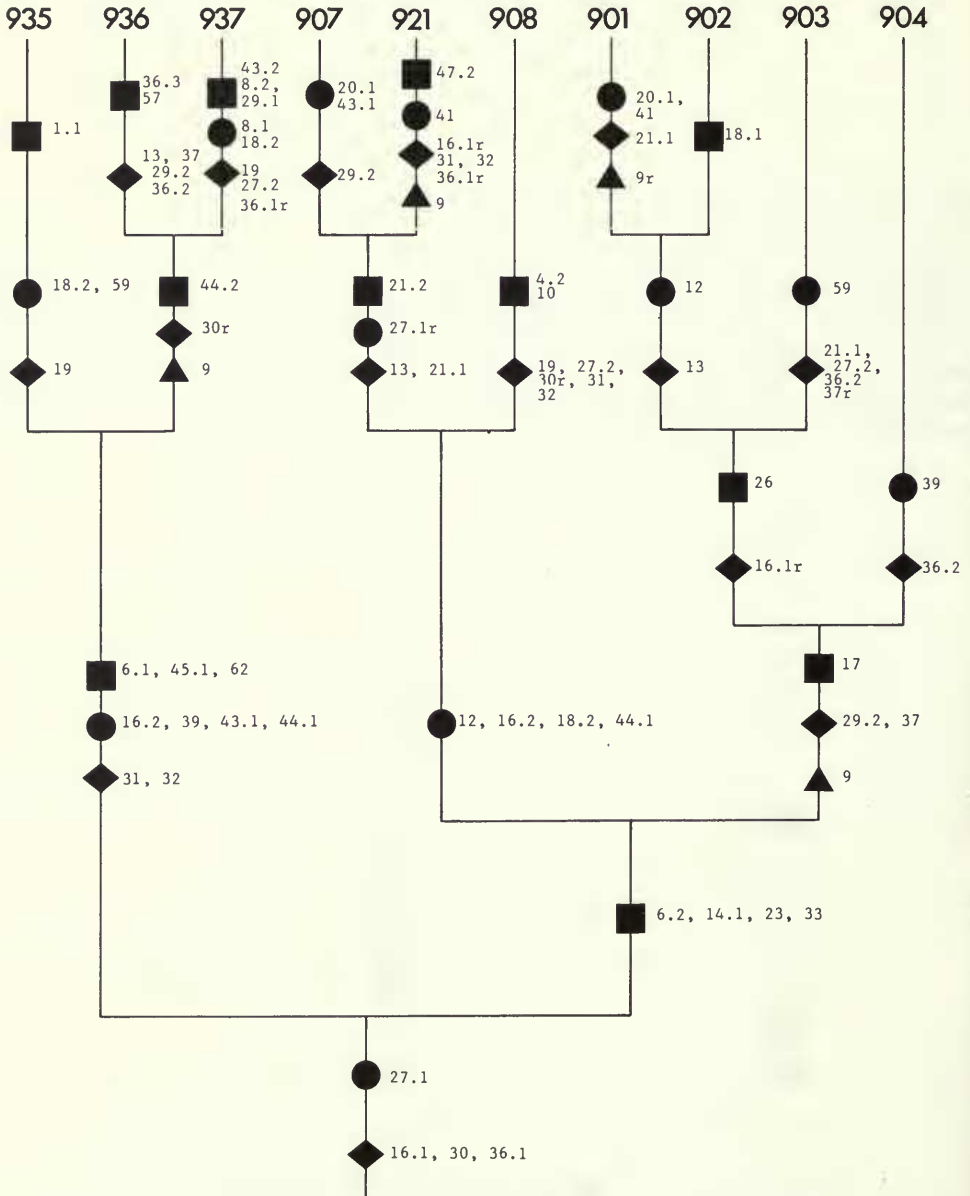


Fig. 13 Most parsimonious cladogram for taxa in the *Thyreodon/Euryophion* complex. Black squares represent uniquely derived characters; circles, apomorphic features derived independently in two lineages; diamonds, in three lineages; squares, in four lineages, or involving four transformations.

undergone reversal), 12 characters (13, 16·1, 19, 21·1, 27·2, 29·2, 30, 31, 32, 36·1, 36·2 and 37) have undergone three transformations, whilst one (9) underwent four. It is noteworthy that the cladogram shows only one of a number of competing cladograms with the same arrangement of taxa and the same number of transformation steps, but different positioning of the homoplastic characters. For example, character 30 is shown as a group apomorphy and is postulated as undergoing reversal in the stem 936/7, and in taxon 908, but it would be equally parsimonious to have suggested that 30 was derived in parallel in stems 901/4, 907/21 and taxon 935. Biologically neither is implausible.

The Stauropoctonus group (Taxa 916, 917, 918)

These three taxa share 29 apomorphies (1·1, 5·1, 5·2, 14·2, 16·1, 16·2, 18·2, 21·1, 22·1, 25·1, 28·1, 28·2, 29·2, 33, 37, 38, 39, 42·1, 42·2, 45·1, 47·1, 49, 51·1, 51·2, 52·1, 52·2, 61·1, 61·2 and 62). Six of these apomorphies (5·1, 5·2, 14·2, 21·1, 42·2 and 52·2) have both lower than average O/E values (0·84, 0·75, 0·83, 0·79, 0·79 and 0·71 respectively) and are shared by relatively few other taxa in the matrix.

Within this group all three possible arrangements of taxa are supported: 916 + 917 by 25·2* and 47·2; 916 + 918 by 1·2*, 36·1', 36·2', 43·1' and 63; 917 + 918 by 57*. All of these eight informative characters have high LeQuesne test failure rates (0·9+) and most are either loss characters or have dubiously assigned polarity, making the choice between arrangements difficult. The most parsimonious would obviously be 916 + 918. Currently 916 and 917 are placed together in *Stauropoctonus* whilst 918 is placed in a separate taxon, *Aulophion* (Cushman, 1947; Townes, 1971). *Aulophion* has traditionally been separated from *Stauropoctonus* by the possession of two autapomorphies, loss of the posterior transverse carina of the mesosternum and absence of the epicnemial carina. This suggests *Stauropoctonus* may be a paraphyletic assemblage. For the present these taxa are treated as an unresolved trichotomy, but their inter-relationship is discussed further below (p. 146). It is sufficient now to state that these three taxa seem to form a closely knit and apparently holophyletic group.

The Enicospilus + Stauropoctonus complex (Taxa 909–919, 924–926, 928–934, 942–947)

This, the largest apparent group of ophionine taxa in the matrix, contains 28 species. (N.B. Taxon 949 which associates with this group in the cluster analysis is exceptional in having the plesiomorphic state of a number of characters usually found in the apomorphic condition in this group (e.g. 25·2, 28·2, 42·1, 51·1, 51·2 and 63). For the present this taxon is excluded from the complex and its position discussed later in the work.) Their nearest neighbours are shown in Table 13. These taxa share four apomorphic features (16·1, 25·1, 28·1 and 51·1). A further 13 characters (22·1, 25·2, 28·2, 33, 36·1, 38, 42·1, 43·1, 45·1, 47·1, 49, 51·2 and 63) are present in the apomorphic state in all except one, two or three taxa. Most of these characters are labelled, often highly, for the species in this group that show the plesiomorphic condition (e.g. 38 for taxon 943 and 47·1 for taxa 944 and 945), suggesting a reversal may have occurred. The exceptions are 22·1 and 33 which are plesiomorphic for taxa 910 and 911. Both are unlabelled in the primary label matrix (Appendix 4). Of the 17 characters listed above as possible apomorphies of this complex, all except 22·1, 33 and 63 occur in the apomorphic condition in a large number of other ophionine taxa in the matrix. Individually therefore, they are not good characters for defining the group. Character 49 is plesiomorphic only in the solitary taxon 926, suggesting 49 may be an apomorphy of all ophionines, and 926, an otherwise specialized species, may have undergone a reversal. Character 16·1 is apomorphic for all taxa except 901–3 and 921; character 25·1 for all except 948 and 951; character 25·2 for all except 918, 920, 922, 923, 938–41, 945, 948, 949 and 951; character 28·1 for all except 939; character 28·2 for all except 908, 920, 923, 928, 938–41, 949 and 951; character 36·1 for all except 909, 917, 920, 921, 922, 937 and 944; character 38 for all except 938, 939, 941, 943, 948 and 951; character 42·1 for all except 905, 922, 925, 938–41 and 948–50; character 43·1 for all except 901–4, 908, 909, 917, 921–22, 925 and 941; character 45·1 for all except 901–4, 907–8, 921, 923, 925–26, 931, 941 and 948; character 47·1 for all except 938, 939, 943, 944, 948 and 951; character 51·1 for all except 920, 922, 939–41 and 949–51; and character 51·2 for all except 920, 922, 932, 938–41 and 948–51. Ten of these characters (25·1, 25·2, 28·1, 28·2, 38, 42·1, 47·1, 49, 51·1 and 51·2) have been stated above (p.

Table 13 The *Enicospilus/Stauropoctonus* complex showing nearest neighbours with numbers of shared derived characters. Conventions as in Table 8. Particularly striking are taxa 944 (an *Enicospilus* species) and 931 (a *Leptophion* species). Both cite their congeners as nearest neighbours, but neither is cited as near neighbours by its congeners.

| | 926 | 925 | 924 | 947 | 946 | 945 | 944 | 943 | 942 | 934 | 933 | 932 | 919 | 915 | 914 | 913 | 912 | 931 | 930 | 929 | 928 | 918 | 917 | 916 | 909 | 910 | 911 | Others |
|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|--------|
| 926 | + | -- | 25 | 25 | 27 | -- | -- | 24 | 27 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- |
| 925 | -- | + | 27 | 28 | 30 | -- | -- | -- | 28 | -- | -- | 24 | -- | -- | -- | -- | -- | -- | -- | -- | -- | 24 | -- | -- | -- | -- | -- | -- |
| 924 | 25 | 27 | + | 27 | 29 | -- | -- | -- | 29 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- |
| 947 | -- | -- | -- | + | 35 | 31 | -- | 31 | 34 | 30 | -- | -- | -- | 30 | 30 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- |
| 946 | -- | -- | -- | 35 | + | -- | -- | -- | 37 | 32 | -- | 32 | -- | -- | 32 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- |
| 945 | -- | -- | -- | 31 | 31 | + | -- | 28 | 31 | 28 | 28 | -- | -- | -- | 28 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- |
| 944 | -- | -- | -- | 24 | 26 | 24 | + | -- | 26 | 24 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- |
| 943 | -- | -- | -- | 31 | 30 | 28 | -- | + | 31 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | 28 | -- | -- | -- | -- | -- | -- |
| 942 | -- | -- | -- | 34 | 37 | 31 | -- | 31 | + | 31 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- |
| 934 | -- | -- | -- | 30 | 32 | -- | -- | -- | 31 | + | -- | 30 | -- | -- | 30 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- |
| 933 | -- | -- | -- | 29 | 29 | -- | -- | -- | 29 | 29 | + | -- | 29 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- |
| 932 | -- | -- | -- | 28 | 32 | -- | -- | -- | 30 | 30 | -- | + | -- | -- | 29 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- |
| 919 | -- | -- | -- | 29 | 29 | -- | -- | -- | 29 | 29 | 29 | -- | + | 32 | 33 | -- | 30 | -- | 29 | -- | 30 | -- | -- | -- | -- | -- | -- | -- |
| 915 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | 32 | + | 36 | 33 | 34 | -- | -- | -- | 31 | -- | -- | -- | -- | -- | -- | -- |
| 914 | -- | -- | -- | -- | 32 | -- | -- | -- | -- | -- | -- | -- | 33 | 36 | + | 33 | 33 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- |
| 913 | -- | -- | -- | 29 | 29 | -- | -- | -- | -- | -- | -- | -- | -- | 33 | 33 | + | 31 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- |
| 912 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | 30 | 34 | 33 | 31 | + | -- | 29 | -- | -- | -- | -- | -- | -- | -- | -- | -- |
| 931 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | 27 | 27 | 27 | -- | -- | + | -- | 27 | 27 | -- | -- | -- | -- | -- | -- | -- |
| 930 | -- | -- | -- | -- | -- | -- | -- | -- | 28 | -- | -- | -- | 29 | 28 | 29 | -- | 28 | -- | + | 29 | 30 | -- | -- | -- | -- | -- | -- | -- |
| 929 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | 30 | 29 | -- | 29 | -- | 29 | + | 29 | -- | -- | -- | -- | -- | -- | -- |
| 928 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | 30 | 31 | 29 | -- | -- | -- | 30 | 29 | + | -- | -- | -- | -- | -- | -- | -- |
| 918 | -- | -- | -- | 28 | -- | -- | -- | 28 | 28 | -- | -- | -- | 28 | -- | -- | -- | -- | -- | -- | -- | -- | + | 30 | 34 | -- | -- | -- | -- |
| 917 | -- | -- | -- | 24 | -- | -- | -- | -- | 24 | -- | -- | -- | 24 | -- | -- | -- | -- | -- | -- | -- | -- | 30 | + | 31 | 25 | -- | -- | -- |
| 916 | -- | -- | -- | 27 | -- | -- | -- | -- | -- | -- | -- | -- | 27 | -- | -- | -- | -- | -- | -- | -- | -- | 34 | 31 | + | 27 | -- | -- | -- |
| 909 | -- | -- | -- | 24 | 24 | -- | -- | -- | -- | -- | -- | -- | -- | 24 | -- | -- | -- | -- | -- | -- | -- | 26 | 25 | 27 | + | -- | -- | 24-936 |
| 910 | -- | -- | -- | -- | 26 | -- | -- | -- | -- | -- | -- | -- | 26 | 28 | 28 | 26 | 26 | -- | -- | 26 | -- | -- | -- | -- | -- | + | -- | 30 |
| 911 | -- | -- | -- | -- | 28 | -- | -- | -- | -- | -- | -- | -- | -- | 28 | 30 | 27 | -- | -- | -- | -- | -- | -- | -- | -- | -- | 30 | + | -- |

90) to be apomorphies of the *Thyreodon/Euryophion* complex, suggesting they are characters that unite the *Enicospilus/Stauropoctonus* and *Thyreodon/Euryophion* generic complexes. Character 16.1 could also be considered an apomorphy of both these major groups if one were to postulate reversal in 901-3 and 921.

Character 22.1 is found in the apomorphic state outside the *Enicospilus/Stauropoctonus* complex only in taxa 920, 940, 949 and 951; character 33 in taxa 901-4, 907-8, 920-22 and 949 and character 63 in 905, 906 and 923. Character 33 is a loss apomorphy and has been cited above as an apomorphy of the *Thyreodon/Dictyonotus* lineage. It is perhaps not unreasonable to postulate parallel loss in the *Enicospilus/Stauropoctonus*, the *Thyreodon/Dictyonotus* and the 920, 922 and 949 lineages. However, this feature, the loss of the umbo, is not apomorphic for taxa 910 and 911 included above in the *Enicospilus* group. It is biologically rather unlikely that the umbo would be lost then redeveloped, so this feature favours placing *Ophiogastrella* (910-11) primitive with respect to the rest of the group. Such a position is also favoured by character 22.1. The apomorphic condition, a lengthened anterior part of the propodeum, is rather unlikely to have undergone reversal.

It is interesting to note that character 22 has two alternative derived states, 22.1 or 22.2. The derived state 22.2 is an apomorphic feature of the *Thyreodon/Euryophion* complex and is only found elsewhere in taxa 906 and 927. The alternative derived state characteristic of the *Enicospilus/Stauropoctonus* group (less *Ophiogastrella*) is also found in very few other taxa (see above). The plesiomorphic condition (0,0) is found in taxa 905, 910, 911, 922, 923, 938, 939, 941 and 948. The character seems to be important in defining two major sister-lineages of the subfamily.

Using the CLIQUE option of PHYLIP eight cliques were found with 12 or more informative characters. These were

| | |
|---|----------------|
| A (12) [18·1, 18·2, 21·1, 22·1, 27·3, 33, 35, 36·3, 42·2, 61·1, 61·2, 64] | Av. O/E = 0·76 |
| B (12) [15·1, 15·2, 18·1, 18·2, 21·1, 22·1, 27·3, 33, 35, 36·3, 42·2, 64] | Av. O/E = 0·75 |
| C (12) [17, 18·1, 18·2, 21·1, 22·1, 27·3, 31, 33, 39, 42·2, 60, 64] | Av. O/E = 0·78 |
| D (12) [15·1, 17, 18·1, 18·2, 21·1, 22·1, 27·3, 31, 33, 42·2, 60, 64] | Av. O/E = 0·77 |
| E (13) [12, 14·2, 17, 18·2, 21·1, 22·1, 27·3, 31, 33, 39, 42·2, 60, 64] | Av. O/E = 0·78 |
| F (12) [12, 15·1, 17, 18·2, 21·1, 22·1, 27·3, 31, 33, 42·2, 55, 64] | Av. O/E = 0·76 |
| G (12) [13, 18·1, 18·2, 21·1, 22·1, 33, 35, 36·3, 42·2, 61·1, 61·2, 64] | Av. O/E = 0·79 |
| H (12) [13, 15·1, 15·2, 18·1, 18·2, 21·1, 22·1, 33, 35, 36·3, 42·2, 64] | Av. O/E = 0·78 |
| A ∩ B ∩ C ∩ D ∩ E ∩ F ∩ G ∩ H = {18·2, 21·1, 22·1, 33, 42·2, 64} | |

The best clique in the sense of the largest is E but this has a lower average O/E value (0·78) than several others. B has the lowest average O/E value with 0·75, closely followed by A and F with 0·76. The remainder have higher values. The cladograms based on the largest clique (E) and the best O/E scoring clique (B) are shown in Figs 14, 15. The cladogram produced from clique B associated the various taxa fairly well with their congeners. Species of *Enicospilus* (942–47), *Dicamptus* (932–34) and the Hawaiian genera (924–26) (regarded by Townes, 1971, as derived *Enicospilus*) cluster together, except for *E. cionobius* (945) which is excluded by having the plesiomorphic condition of 15·2 (possibly a reversal). *Laticoleus* (912–15) and *Leptophion* (928–30) species form a separate cluster as do the *Stauropoctonus* group (916–18) plus *Lepiscelus* (909). The cladogram derived from clique E has more confusing groupings, uniting some species of *Enicospilus* and *Laticoleus* (character 17) or defining a clade containing *Dicamptus neavei*, *Leptophion tetus* and *Abanchogastra hawaiiensis* (character 12). The heterogeneous collection of species united by character 14·2 includes representatives of *Dicamptus*, *Enicospilus*, *Laticoleus* and *Leptophion*; other species of these genera are excluded. The largest clique, E, is therefore not considered particularly useful in this case; clique B appears to be a better indicator of relationship. It is noteworthy that clique B is more informative ($s = 0·681$) than clique E ($s = 0·632$).

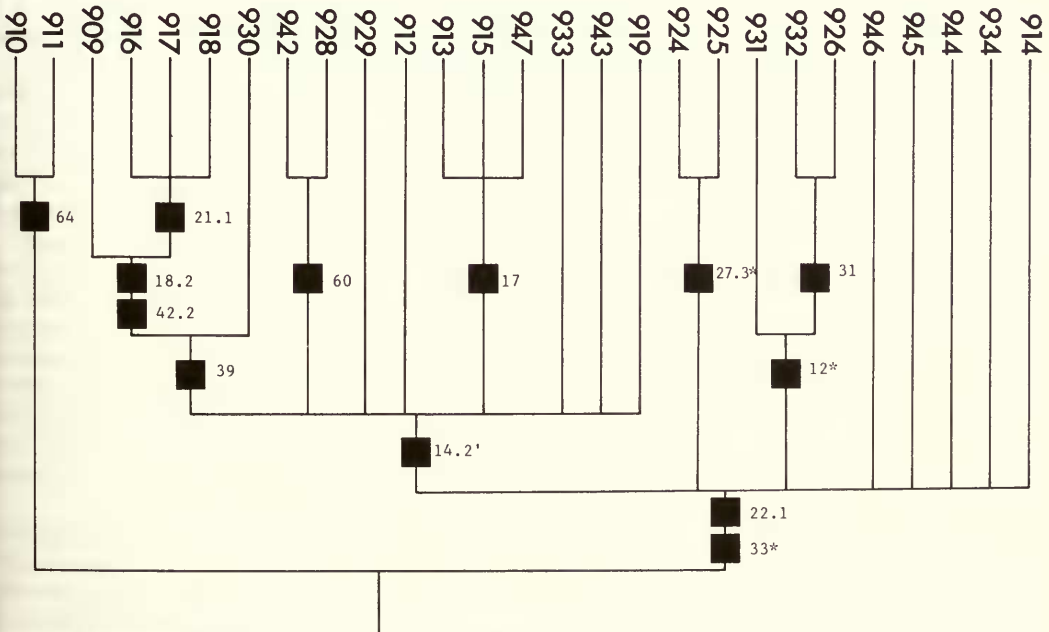


Fig. 14 Cladogram for taxa in the *Enicospilus/Stauropoctonus* complex based on the largest clique (E).

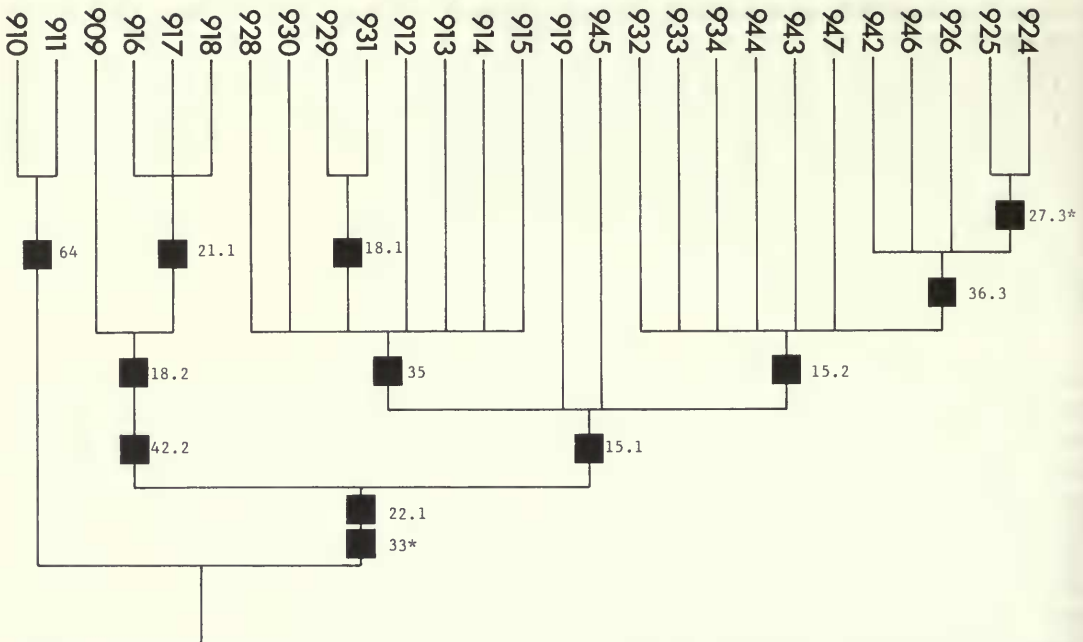


Fig. 15 Cladogram for taxa in the *Enicospilus/Stauropoc-tonus* complex based on the favoured clique (B).

It is notable that the intersect of these cliques includes several characters previously considered to be good indicators of phylogenetic relationship (Cushman, 1947; Townes, 1971). Three (18.2, 21.1 and 42.2) support the group 909 + 916–18, whilst two others (22.1 and 33) place *Ophiogastrella* (910–11), primitive to the other taxa. Character 64 is an autapomorphy of *Ophiogastrella*.

A LeQuesne test was undertaken on the *Enicospilus/Stauropoc-tonus* data set and the O/E values are given in Table 14. Stepwise elimination of all characters scoring worse than 1.00 (a total of 15) resulted in considerable cleaning up. The overall ratio improved from 0.89 to 0.74. Amongst the scoring characters the most striking changes in rank occurred to 1.2 which rose from thirty-fifth to eleventh position, and 62 which dropped from thirty-first place to position forty-three. Amongst the best scoring characters 42.2 and 18.2 rose from fourteenth and sixteenth positions to seventh and eighth positions (Table 15). Using the S option of FOURS the data set was reorganized with characters ranked as per O/E value after removal of the 15 most discordant characters (Table 16). It can be seen that the characters with the lowest O/E values, 22.1 and 33, exclude *Ophiogastrella* (910–11) whilst 64 is an autapomorphy of this genus. A number of other characters may be postulated as apomorphies of *Ophiogastrella*, though all apparently have been derived in parallel elsewhere. Characters 18.2 and 42.2 support the *Stauropoc-tonus* group + 909, whilst 21.1 supports just the former. Character 1.2 is incompatible with 21.1. Initially it had a poor O/E score (0.93 compared with 0.54 for 21.1) but progressive elimination of the poorest characters produced rapid ‘clean-up’ until with 15 characters eliminated it scored 0.57 compared with 0.34 for 21.1. With only the 18 best characters left in the matrix both taxa scored equally 0.13. A considerable number of slightly homoplastic characters (e.g. 5.1, 5.2, 37, 52.1) support 21.1 but no other character supports 1.2 and it is for this reason that one would prefer the arrangement supported by the former character.

Several other characters support the *Stauropoc-tonus* + 909 group but necessitate postulating parallel derivation in other places. These include 1.1 (parallelism in 925 and 945), 39 (parallelism in 930), 61.1 (parallelism in 924–26 and 942–47). Many of these parallelisms are also suggested in the reduced labels matrix (Appendix 6), e.g. taxon 930 for character 39 acquires almost half of its total number of labels and taxa 925 and 945 are quite highly labelled for character 1.1.

Table 14 Results of a LeQuesne test on the *Enicospilus/Stauropogon* data set. Conventions as in Table 2.

| Character number: | incompatibilities | observed | expected | O/E ratio |
|-------------------------------------|-------------------|------------------|--------------------------|-----------|
| <u>1.1</u> : 40 | 42.7 | 0.94 | <u>1.2</u> : 27 | 29.2 0.93 |
| <u>5.1</u> : 45 | 50.5 | 0.89 | <u>5.2</u> : 41 | 42.3 0.97 |
| <u>12</u> : 27 | 29.7 | 0.91 | <u>13</u> : 10 | 19.9 0.50 |
| <u>15.2</u> : 39 | 50.0 | 0.78 | <u>16.2</u> : 48 | 40.1 1.20 |
| <u>18.2</u> : 27 | 35.5 | 0.76 | <u>19</u> : 27 | 19.9 1.35 |
| <u>21.1</u> : 16 | 29.7 | 0.54 | <u>22.1</u> : 5 | 19.9 0.25 |
| <u>25.2</u> : 26 | 19.9 | 1.30 | <u>27.1</u> : 41 | 46.2 0.89 |
| <u>29.2</u> : 34 | 43.2 | 0.79 | <u>30</u> : 22 | 19.9 1.10 |
| <u>35</u> : 28 | 47.6 | 0.59 | <u>36.1</u> : 33 | 28.6 1.15 |
| <u>37</u> : 50 | 49.0 | 1.02 | <u>39</u> : 36 | 40.1 0.90 |
| <u>43.1</u> : 32 | 29.0 | 1.10 | <u>43.2</u> : 50 | 48.3 1.03 |
| <u>45.1</u> : 30 | 29.0 | 1.04 | <u>45.2</u> : 45 | 49.4 0.91 |
| <u>47.2</u> : 52 | 50.5 | 1.03 | <u>48.1</u> : 47 | 50.5 0.93 |
| <u>52.2</u> : 40 | 42.3 | 0.95 | <u>55</u> : 25 | 35.8 0.70 |
| <u>59</u> : 48 | 51.7 | 0.93 | <u>60</u> : 17 | 19.9 0.85 |
| <u>62</u> : 36 | 40.1 | 0.90 | <u>64</u> : 5 | 19.9 0.25 |
| | | | <u>3</u> : 33 | 47.6 0.69 |
| | | | <u>6.1</u> : 28 | 19.9 1.40 |
| | | | <u>14.2</u> : 43 | 51.5 0.84 |
| | | | <u>17</u> : 25 | 29.7 0.84 |
| | | | <u>20.1</u> : 38 | 34.9 1.09 |
| | | | <u>24.1</u> : 49 | 48.1 1.02 |
| | | | <u>27.2</u> : 41 | 46.2 0.89 |
| | | | <u>31</u> : 19 | 19.9 0.95 |
| | | | <u>36.2</u> : 44 | 44.3 0.99 |
| | | | <u>40</u> : 34 | 47.6 0.71 |
| | | | <u>44.1</u> : 55 | 48.2 1.14 |
| | | | <u>47.1</u> : 15 | 19.5 0.77 |
| | | | <u>48.2</u> : 39 | 46.6 0.84 |
| | | | <u>52.1</u> : 45 | 48.1 0.94 |
| | | | <u>56</u> : 28 | 19.9 1.40 |
| | | | <u>57</u> : 35 | 35.8 0.98 |
| | | | <u>61.1</u> : 35 | 50.7 0.69 |
| | | | <u>61.2</u> : 40 | 50.5 0.79 |
| | | | <u>7.2</u> : 39 | 51.5 0.76 |
| | | | <u>15.1</u> : 37 | 42.3 0.88 |
| | | | <u>18.1</u> : 11 | 19.7 0.56 |
| | | | <u>20.2</u> : 46 | 50.1 0.92 |
| | | | <u>24.2</u> : 50 | 44.7 1.12 |
| | | | <u>27.3</u> : 11 | 19.1 0.58 |
| | | | <u>33</u> : 5 | 19.9 0.25 |
| | | | <u>36.3</u> : 25 | 38.8 0.64 |
| | | | <u>42.2</u> : 27 | 35.8 0.75 |
| | | | <u>44.2</u> : 43 | 35.0 1.23 |
| | | | <u>47.2</u> : 15 | 19.5 0.77 |
| | | | <u>52.2</u> : 45 | 48.1 0.94 |
| | | | <u>57</u> : 35 | 35.8 0.98 |
| | | | <u>61.2</u> : 40 | 50.5 0.79 |
| Grand total- | 1035 observed, | 1161.2 expected. | Overall O/E ratio = 0.89 | |
| Ranking ratio of scoring characters | | | | |
| 22.1 | 33 | 64 | 13 | 21.1 |
| 61.2 | 14.2 | 46 | 48.2 | 17 |
| 1.1 | 52.2 | 31 | 5.2 | 57 |
| 16.2 | 44.2 | 25.2 | 19 | 6.1 |
| 27.3 | 35 | 36.3 | 61.1 | 3 |
| 55 | 40 | 42.2 | 7.2 | 18.2 |
| 47.1 | 15.2 | 29.2 | | |
| 60 | 15.1 | 27.1 | 27.2 | 5.1 |
| 39 | 62 | 12 | 45.2 | 20.2 |
| 1.2 | 59 | 48.1 | 52.1 | |
| 37 | 47.2 | 43.2 | 45.1 | 20.1 |
| 4.1 | 43.1 | 30 | 24.2 | 44.1 |
| 36.1 | 36.1 | 36.1 | 36.1 | 36.1 |

Table 15 Results of a LeQuesne test on the *Enicospilus/Stauropogon* data set after progressive removal of 15 highest scoring characters (56, 19, 6.1, 25.2, 44.2, 16.2, 24.2, 44.1, 30, 57, 24.1, 43.2, 36.1, 45.1, 36.2). Conventions as in Table 2.

| Character number: | incompatibilities | observed | expected | O/E ratio |
|-------------------------------------|-------------------|----------------|--------------------------|-----------|
| <u>1.1</u> : 26 | 33.2 | 0.78 | <u>1.2</u> : 13 | 23.0 0.57 |
| <u>5.1</u> : 33 | 38.7 | 0.85 | <u>5.2</u> : 29 | 32.8 0.89 |
| <u>13</u> : 7 | 15.8 | 0.44 | <u>14.2</u> : 32 | 39.7 0.81 |
| <u>17</u> : 18 | 23.5 | 0.76 | <u>18.1</u> : 9 | 15.5 0.58 |
| <u>20.2</u> : 32 | 38.4 | 0.83 | <u>21.1</u> : 8 | 23.5 0.34 |
| <u>27.2</u> : 30 | 35.5 | 0.85 | <u>27.3</u> : 6 | 14.9 0.40 |
| <u>33</u> : 1 | 15.8 | 0.06 | <u>35</u> : 20 | 36.9 0.54 |
| <u>39</u> : 22 | 31.4 | 0.70 | <u>40</u> : 25 | 36.9 0.68 |
| <u>45.2</u> : 34 | 38.7 | 0.88 | <u>46</u> : 32 | 38.7 0.83 |
| <u>48.1</u> : 33 | 38.7 | 0.85 | <u>48.2</u> : 29 | 35.9 0.81 |
| <u>55</u> : 20 | 28.3 | 0.71 | <u>59</u> : 36 | 39.9 0.90 |
| <u>61.2</u> : 28 | 38.7 | 0.72 | <u>62</u> : 29 | 31.4 0.92 |
| | | | <u>3</u> : 23 | 36.9 0.62 |
| | | | <u>7.2</u> : 27 | 39.7 0.68 |
| | | | <u>15.1</u> : 23 | 32.8 0.70 |
| | | | <u>18.2</u> : 13 | 28.0 0.46 |
| | | | <u>22.1</u> : 1 | 15.8 0.06 |
| | | | <u>29.2</u> : 25 | 33.7 0.74 |
| | | | <u>36.3</u> : 17 | 31.4 0.54 |
| | | | <u>42.2</u> : 13 | 28.3 0.46 |
| | | | <u>47.1</u> : 10 | 15.3 0.65 |
| | | | <u>52.1</u> : 33 | 37.0 0.89 |
| | | | <u>60</u> : 14 | 15.8 0.89 |
| | | | <u>64</u> : 1 | 15.8 0.06 |
| | | | <u>12</u> : 20 | 23.5 0.85 |
| | | | <u>15.2</u> : 27 | 38.3 0.70 |
| | | | <u>20.1</u> : 24 | 27.4 0.88 |
| | | | <u>27.1</u> : 30 | 35.5 0.85 |
| | | | <u>31</u> : 14 | 15.8 0.89 |
| | | | <u>37</u> : 36 | 37.9 0.95 |
| | | | <u>43.1</u> : 22 | 23.5 0.93 |
| | | | <u>47.2</u> : 38 | 38.8 0.98 |
| | | | <u>52.2</u> : 30 | 32.8 0.91 |
| | | | <u>61.1</u> : 24 | 38.9 0.62 |
| Grand total- | 522 observed | 708.4 expected | Overall O/E ratio = 0.74 | |
| Ranking ratio of scoring characters | | | | |
| 22.1 | 33 | 64 | 21.1 | 27.3 |
| 15.2 | 55 | 61.2 | 29.2 | 17 |
| 31 | 60 | 52.1 | 59 | 52.2 |
| 62 | 43.1 | 37 | 4.1 | 47.2 |
| 14.2 | 48.2 | 46 | 20.2 | 27.1 |
| 27.2 | 12 | 5.1 | 48.1 | 20.1 |
| 45.2 | 45.2 | 5.2 | | |

Using the CLIQUE option of PHYLIP on the data set with the basal taxa (910–11, 909, 916–18) removed revealed the existence of four cliques with eight or more informative characters. These are

A (8) [4·1, 5·1, 18·1, 27·3, 35, 36·3, 61·1, 61·2]

Av. O/E = 0·81

B (9) [4·1, 5·1, 27·1, 27·2, 27·3, 35, 36·3, 61·1, 61·2]

Av. O/E = 0·83

C (8) [4·1, 5·1, 13, 18·1, 35, 36·3, 61·1, 61·2]

Av. O/E = 0·86

D (9) [4·1, 5·1, 13, 27·1, 27·2, 35, 36·3, 61·1, 61·2]

Av. O/E = 0·87

$A \cap B \cap C \cap D = \{4·1, 5·1, 35, 36·3, 61·1, 61·2\}$

These sets support very similar cladograms; the favoured one, with the lowest average O/E, is shown in Fig. 16, but all are similar in showing two large groups (912–15 + 928–31 and 924–26 + 942–47) and leaving taxa 919 and 932–34 unresolved.

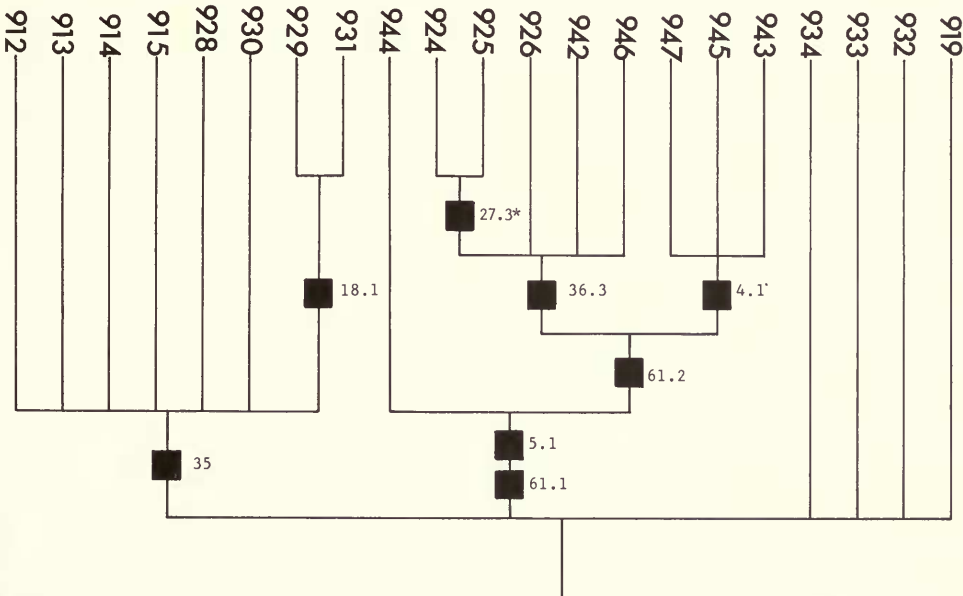


Fig. 16 Cladogram for taxa in the *Enicospilus/Stauropctonus* complex less taxa 909–911 and 916–8, based on the favoured clique (A).

Using the WAGNER option of PHYLIP several attempts were made to construct the shortest rooted tree possible. The minimum length tree (Fig. 17) necessitated 242 transformation steps.

Both parsimony and compatibility analyses have certain similarities. Both taxa 909 + 916–18 formed a group primitive to most other taxa whilst *Enicospilus* (942–47) and *Dicamptus* (932–34) are amongst the most specialized taxa and separate from *Laticoleus* (912–15) and *Leptophion* (928–31). However, the Wagner parsimony method usually separated the Hawaiian taxa (924–26) as a relatively primitive, discrete group but placed *Ophiogastrella* (910–11) well in the *Enicospilus/Dicamptus/Leptophion/Laticoleus* complex. Compatibility methods suggested the reverse. To assess the relative merits of these alternative arrangements it is necessary to evaluate the characters upon which they are based. As mentioned above, the exclusion of taxa 910 and 911 is based on characters 15·1, 22·1 and 33 which are present in the apomorphic condition in all other taxa. The former two are striking structural modifications and whilst the latter is a loss apomorphy, it is an unusual reduction (when considered for the family as a whole). There is no apparent functional reason why these characters should be linked, so their congruence can be viewed as strong evidence for excluding 910–11 as the first branch. However, 910 and 911 do have a number of apomorphies in common with many other taxa in the group,

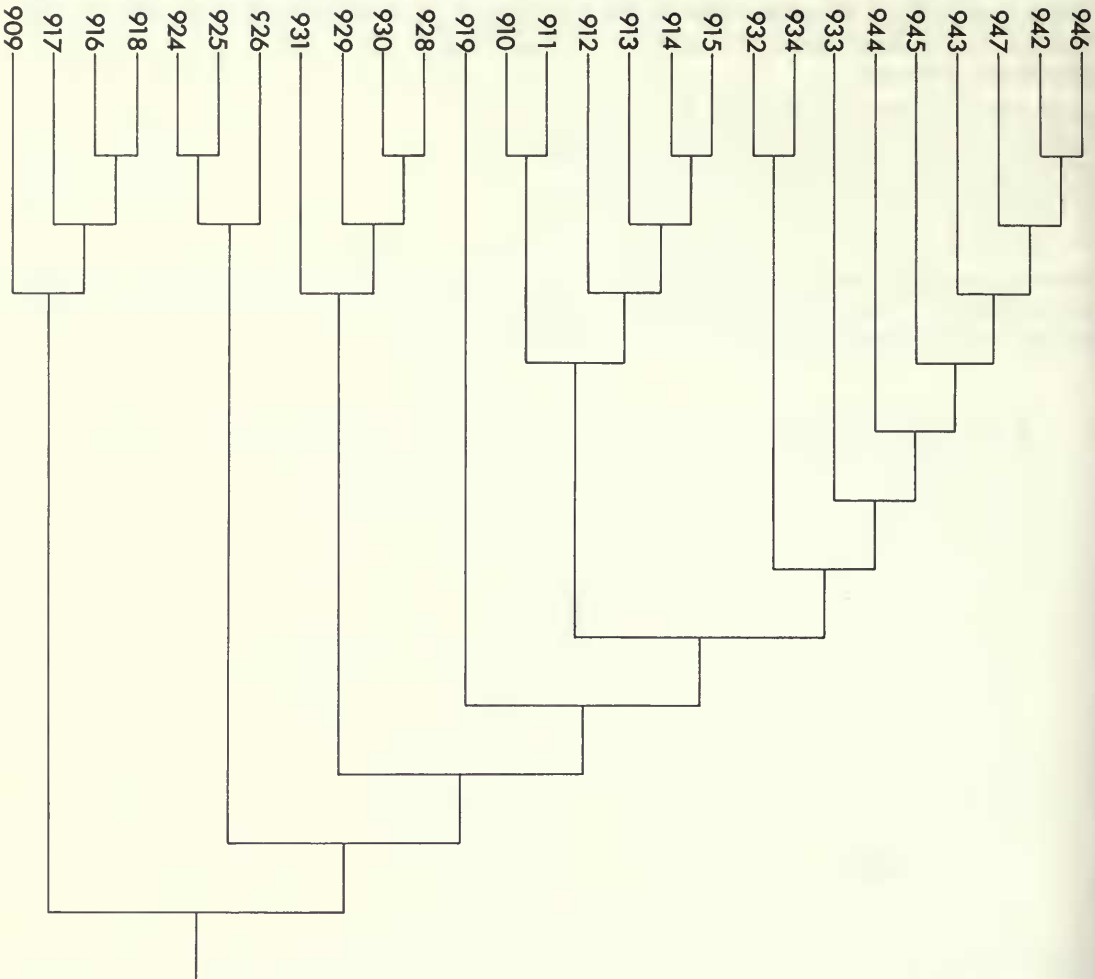


Fig. 17 Minimum length cladogram produced by Wagner parsimony analysis of the *Enicospilus/Stauropogon* complex. This tree requires 242 transformation steps.

especially the *Laticoleus/Leptophion* complex (e.g. characters 7·2, 27·1, 27·2, 20·1) which it must be assumed has been derived in parallel if *Ophiogastrella* is indeed the most primitive branch.

The Wagner analysis united all taxa excluding the *Stauropogon*/909 complex on the basis of characters 15·1, 36·2 and 43·1. The former has been postulated as having undergone reversal in the stem 910 + 911 so cannot be considered a group apomorphy, whilst 36·2 is highly homoplastic in any favoured arrangement, and in the minimum length tree necessitates six transformations that include being developed, lost and subsequently redeveloped. In fact, this character is also present in the apomorphic condition in some *Stauropogon* (916, 918), and it is not stretching credibility to consider it an apomorphy of the entire group here being analysed, and postulate reversal in taxa 909 and 917. This hypothesis involves only a single additional transformation step, and would seem biologically more feasible than the gain-loss-gain scheme favoured by the Wagner analysis. The character itself, relative position of two wing veins, has not been used in higher classification, though it is of considerable use in separating species (Gauld & Mitchell, 1978), and has doubtfully assigned polarity. It is also amongst the very worst characters suggested by the original LeQuesne test (see Table 6). The third character, 43·1, is found widely in the apomorphic condition throughout the Ophioninae. Either it has been

derived in parallel in the *Euryophion* group, in most *Ophion* and related taxa and in certain members of the present group, or it is an apomorphy of the Ophioninae and the apparently plesiomorphic state of most *Stauropoctonus* group taxa represents a further apomorphy. Initially the polarity of this character was considered to be tentatively assigned (p. 77). Elsewhere in the Ichneumonidae, although reliance is often placed on character 43·1 in generic keys, it is variable in most higher taxa (cf. Pimplinae in Townes, 1969), suggesting it is a highly homoplastic feature.

Other characters involved in placing *Ophiogastrella* high up the tree are 7·2, 20·2, 27·1, 27·2, 37, 43·2, 45·2, 48·1 and 59. Of these, 7·2 and 59 are highly homoplastic, gain-loss-gain characters which seem biologically implausible, and they also have dubious polarity assignment. Character 45·2 is postulated as having undergone reversal in the stem 910 + 911 so there remains five reasonably robust apomorphies uniting *Ophiogastrella* with the most specialized taxa (20·2, 27·1, 27·2, 43·2 and 48·1). Considered individually, all of these characters are rather 'weak'. The remarks made above about 43·1 can also be applied to 43·2; the loss apomorphies 27·1 and 27·2 have identical state distributions in this group and should perhaps be considered as a single feature, the loss of the posterior mesosternal transverse carina. This carina has been lost, presumably independently, in other ophionine evolutionary lines (e.g. *Ophion*, some *Leptophion*, some of the *Stauropoctonus* group) and has commonly been lost in many ichneumonid evolutionary lineages outside the subfamily under consideration. As a consequence it is not a character which seems to unite convincingly *Laticoleus* (912–5) with *Ophiogastrella*. It is interesting to note that there is at least some degree of correlation between the presence or absence of this carina and the type of habitat occupied. In groups where it is usually absent (e.g. the Phygadeuontinae), species inhabiting very wet areas have the carina complete. In the subfamily mentioned this includes common species of *Paraphylax*, *Amauromorpha* and *Apsilops* found in Old World rice padi. In the Anomaloninae the two closely related genera *Therion* and *Heteropelma* differ in this feature; the former is characteristically found on dry open areas, whilst most *Heteropelma* species occur in more humid woodlands (Gauld, 1976). In the Ophioninae the carina is always present in those species found in humid rain forests (e.g. most *Enicospilus*, *Leptophion* and *Dicamptus*) but is incomplete in species favouring drier, more exposed habitats (e.g. some Australian *Leptophion*, most *Ophion*). Both *Ophiogastrella* species and *Laticoleus* seem to favour drier forest habitats than *Leptophion*.

Character 20·2, the development of scutellar carinae, has probably been derived independently in several evolutionary lineages (e.g. some species of *Ophion* and *Leptophion* (Gauld & Mitchell, 1981)), but it also appears to have undergone reversal in other groups (e.g. in taxon 944 and also *Enicospilus arduus* (Gauld & Mitchell, 1978)). It would be only slightly less parsimonious to suggest that the presence of complete scutellar carinae is an apomorphy of the entire *Enicospilus/Stauropoctonus* complex, and to suggest that it has been lost in a few lineages. Certainly the shared presence of these carinae is not a convincing character for uniting *Ophiogastrella* with other genera.

The remaining character, 48·1, is a difference in relative lengths of wing veins and its apomorphic state is found scattered throughout the subfamily.

To summarize therefore, the decision on where to position *Ophiogastrella* hinges on two character sets, one of three unusual and fairly convincing apomorphies (15·1, 22·1 and 33) versus five widely distributed, and thus unconvincing, apomorphies (20·2, 27·1, 27·2, 43·2 and 48·1). The Wagner method, in attempting to minimize tree length, opts for including *Ophiogastrella* amongst the most derived species, whilst the compatibility method favours treating it as the most primitive taxon, thus eliminating homoplasy in three characters (22·1, 33 and 15·1) as the other characters are mutually incompatible.

The position of the Hawaiian genera (924–6) also presents a problem. In the parsimony dendrogram (Fig. 17) the five characters defining the stem 924 + 925 + 926 (5·1, 15·2, 36·3, 61·1 and 61·2) also define at least part of the *Enicospilus* + *Dicamptus* branch (932–4 + 942–7) suggesting the Hawaiian genera could be placed on the larger branch, as in the compatibility dendrogram. The parsimony method has excluded the Hawaiian genera on the basis of characters 7·2, 20·2, 40, 43·2, 45·2, 46, 48·1 and 59. Of these 7·2 and 59 are the biologically

implausible gain/loss/gain characters with dubiously assigned polarity, so the real choice has to be made between the two character sets 5·1, 15·2, 36·3, 61·1 and 61·2 versus 20·2, 40, 43·2, 45·2, 46 and 48·1.

Considering the first set first, characters 5·1, 61·1 and 61·2 are all mandible characters. The apomorphic state of all three is elsewhere only found in taxa 916–8 and 942–7 (excluding 944). Although this character set has almost certainly been derived independently in *Stauropogonius/Aulophion* and *Enicospilus* it is not found elsewhere in the Ophioninae. It is of very rare occurrence in other parts of the family, and where it does occur it is usually characteristic of a group of genera e.g. the Orthocentrinae (Townes, 1971) and the *Xanthopimpla/Echthromorpha* group of Pimplini (Townes, 1969). Character 15·2, a completely concealed spiracular sclerite, is found in virtually all species of *Enicospilus* and *Dicamptus*. Elsewhere it is found in the derived condition only in the Hawaiian genera, in a few species of *Leptophion* and in the aberrant monotypic genus *Sicophion* (922). The final character in this set, 36·3, an extreme reduction in the length of a wing vein, is only found in a very few taxa, notably (in the matrix) the Hawaiian genera, some *Enicospilus*, *Euryophion* and *Xylophion*. Elsewhere in the Ophioninae it only occurs in some *Dicamptus* and one aberrant *Laticoleus*.

The second and alternative character set (20·2, 40, 43·2, 45·2, 46 and 48·1) has partially been considered above where characters 20·2, 43·2 and 48·1 have been suggested to be rather poor indicators of phylogenetic affinity. Two of the Hawaiian genera show the derived state of 48·1, so it would be equally parsimonious to postulate that a reversal had occurred in one Hawaiian genus, as opposed to parallel derivation in the subgroup of two Hawaiian taxa and the major line in the larger group. The remaining characters all refer to the fore wing, in particular the antero-distal part of the discosubmarginal cell and the adjacent vein, *Rs*+2*r*. The apomorphic conditions of characters 40, 45·2 and 46 are the most characteristic features of *Enicospilus/Dicamptus*, though the same combination is also found in a very few other taxa (e.g. *Riekophion* species). Several species of *Enicospilus* may have one or more characters in the plesiomorphic state (e.g. the *E. senescens* species-group (Gauld & Mitchell, 1978)), but the trace features found in one or two species suggests this condition represents a reversal. This suite of characters does seem therefore to be good evidence for excluding the Hawaiian taxa from the *Enicospilus* lineage. However, the plesiomorphic condition of all three of these characters occasionally is found in some *Enicospilus* species inhabiting oceanic islands, and in these cases it can be seen that a reversal has occurred as related taxa still have the apomorphic states. For example, the three species *E. vidus*, *E. ditor* and *E. donor* form a closely interrelated group on the Galapagos Islands (Gauld & Carter, 1983). They belong to the *E. capensis* species-group and probably have evolved from a migrant South American species, all of which have the apomorphic condition for characters 40, 45·2 and 46, as has *E. vidus*. In *E. donor* they all are plesiomorphic, whilst in *E. ditor* intermediate conditions exist. This strongly suggests reversal has occurred. A similar case can be demonstrated for Hawaiian *Enicospilus* (see Cushman, 1944). The majority of *Enicospilus* species are both synchronous and sympatric with numerous congeners. The three characters are developed in such a way as to form a distinctive, species-specific pattern (especially the exact shape of the sclerite, character 46) (see figs 384–641 in Gauld & Mitchell, 1981). In areas where few species occur, such as deserts, there is considerable variation within a species in the exact expression of these characters. Possibly their reversal on oceanic islands is facilitated by a reduction in selection pressure that favours uniformity in areas of high possible interspecific interaction. It is possible that the apparent plesiomorphic condition of these characters in the Hawaiian genera is also a reversal, though in this case no definite close relatives are known.

The remaining character in the second set, 48·1, refers to the relative lengths of veins 3*r*–*m* and *M*. The apomorphic condition has previously been used only to characterize species and both states can be found in most genera, suggesting it is a rather homoplastic feature.

To sum up, once again the Wagner method positioned a group on the basis of the larger set and again biological evidence suggests that perhaps this is incorrect and the position indicated by the compatibility method is more plausible.

The parsimony analysis united all species of *Enicospilus* (942–47) into a single clade but *Dicamptus* was paraphyletic with respect to this. This is not surprising as traditionally *Enico-*

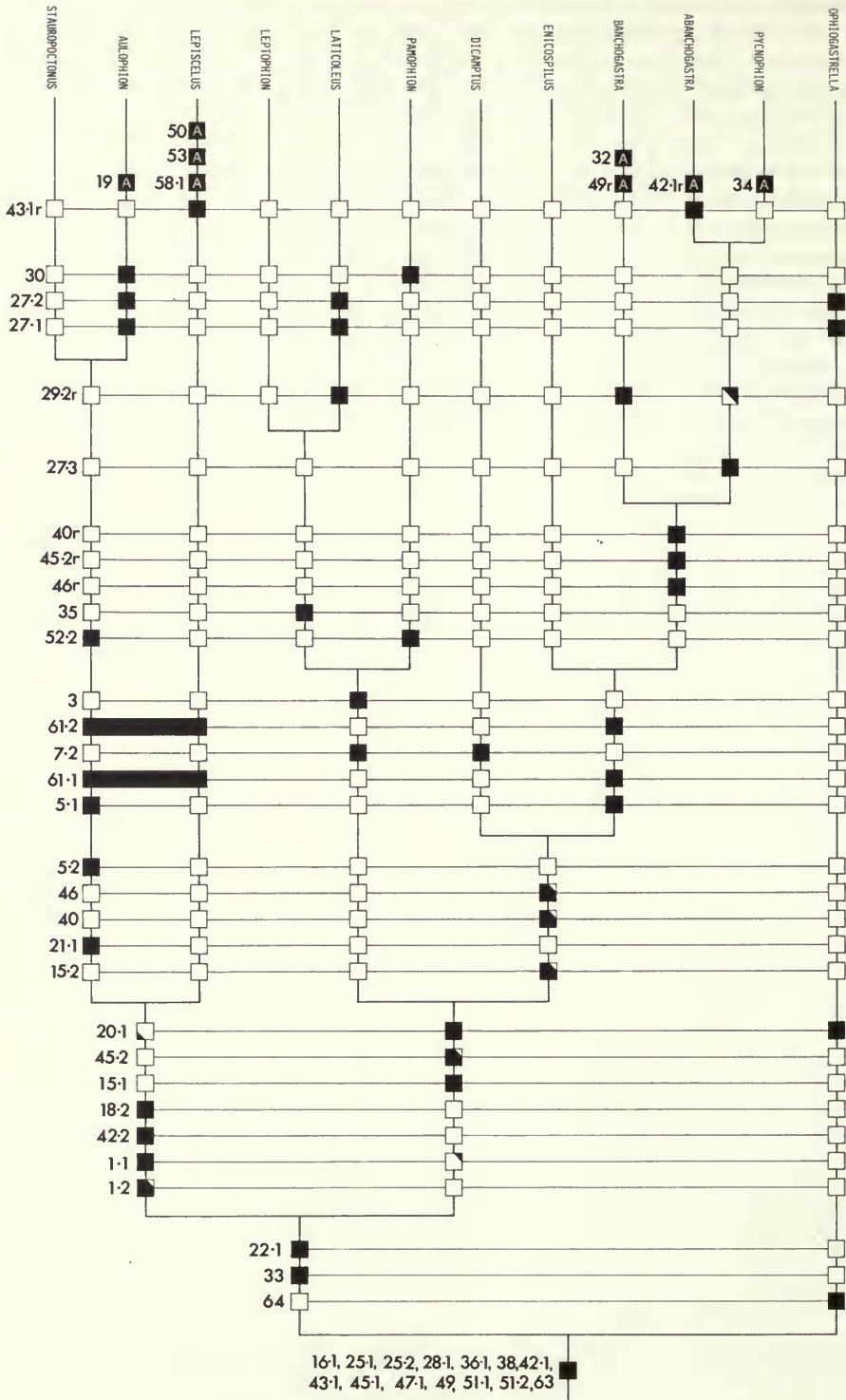


Fig. 19 Cladogram showing putative phylogenetic relationships between the genera of the *Enicospilus/Stauropoctonus* complex as supported by the least homoplastic characters.

species within genera disregarded (and the object of this part of the analysis is to establish the phylogenetic relationships of the genera) and single exceptional character scores, that are almost certainly incidences of homoplasy (e.g. 15·2 in taxon 945; 61·2 in taxon 944), ignored. This simplified cladogram together with supporting characters is illustrated in Fig. 19. Essentially it is the same arrangement as Fig. 18.

This cladogram suggests that *Stauropoctonus* is paraphyletic with respect to *Aulophion*, *Leptophion* is paraphyletic with respect to *Laticoleus* and *Enicospilus* is paraphyletic with respect to the *Pycnophion/Abanchogastra/Banchogastra* lineage.

The major groups and their relationship with the unassigned taxa

The inter-relationship of the two major generic complexes

The *Enicospilus/Stauropoctonus* complex has been defined above as a holophyletic group on the basis of 17 apomorphies (16·1, 22·1, 25·1, 25·2, 28·1, 28·2, 33, 36·1, 38, 42·1, 43·1, 45·1, 47·1, 49, 51·1, 51·2 and 63) (though *Ophiogastrella* is primitive in respect of two, 22·1 and 33) and the *Thyreodon/Euryophion* complex has similarly been defined by a possible 19 apomorphies (2, 7·1, 22·2, 24·1, 24·2, 25·1, 25·2, 28·1, 28·2, 38, 42·1, 42·2, 47·1, 49, 51·1, 51·2, 54, 58·1 and 61·1). Ten of these apomorphic features (25·1, 25·2, 28·1, 28·2, 38, 42·1, 47·1, 49, 51·1 and 51·2) are common to both sets, suggesting a sister group relationship. Of the apomorphies remaining for defining the *Thyreodon/Euryophion* lineage, three (24·1, 24·2 and 61·1) occur extensively in various species-groups and species in the *Enicospilus/Stauropoctonus* complex, thus weakening their credibility as characters defining the former lineage. Character 42·2 has apparently been derived in parallel in the *Stauropoctonus* line, but the remaining five features (2, 7·1, 22·2, 54 and 58·1) are robust characters that strongly support the monophyly of the *Thyreodon/Euryophion* lineage. Of the six remaining apomorphies defining the *Enicospilus/Stauropoctonus* lineage (16·1, 22·1, 33, 36·1, 45·1 and 63) two (22·1 and 33) exclude *Ophiogastrella*; the apomorphic state of 33 has also been derived in parallel in the *Thyreodon* line. The derived states of characters 16·1 and 36·1 occur in most species of the *Thyreodon/Euryophion* complex, suggesting they are group apomorphies, whilst the derived state of 45·1 also occurs, in parallel, in *Euryophion*. Character 63 is the single convincing apomorphy supporting the monophyly of the *Enicospilus/Stauropoctonus* complex. A cladogram showing the putative phylogeny of these taxa is shown in Fig. 20.

The position of the unassigned taxa

The position of the remaining taxa (905, 906, 920, 922, 923, 927, 938–41 and 948–51) can now be considered in relation to the robust arrangement of the majority of ophionine taxa presented above. To reduce the data matrix to more manageable proportions a number of hypothetical taxonomic units (HTUs) were constructed to represent genera reasonably placed in the earlier part of the work. Scores were assigned to these HTUs by marking each character with the condition found in the majority of species of the genus (including all taxa examined in earlier taxonomic studies (Gauld, 1977; Gauld & Mitchell, 1978, 1981) but not included in the primary data matrix). This method of scoring, rather than deducing a hypothetical ancestor, was adopted because of the high incidence of homoplasy. This idiosyncrasy is unlikely to alter any cladistic arrangement significantly, whereas the assumption that the group-ancestor has a particular character present in the plesiomorphic condition, based on occasional incidence of the occurrence of the plesiomorphic (and possibly reversed) condition in some members of the group, could result in considerable alteration to the position assigned to the group. The HTUs utilized are 960 (*Laticoleus*), 961 (*Ophiogastrella*), 962 (*Leptophion*), 963 (*Stauropoctonus*), 964 (*Thyreodon/Dictonotus*), 965 (*Euryophion*), 967 (*Dicamptus*), 968 (*Enicospilus*). [N.B. There is no 966.] The character scores of these HTUs are given in Appendix 7.

The results of a LeQuesne test on taxa 905, 906, 920, 922, 923, 927, 938–41, 948–51 and 960–68 are given in Table 17. The overall O/E value is strikingly high (0·90), indicating the extremely homoplastic nature of this data set. Perusal of the labels matrix (Appendix 8) shows that a large

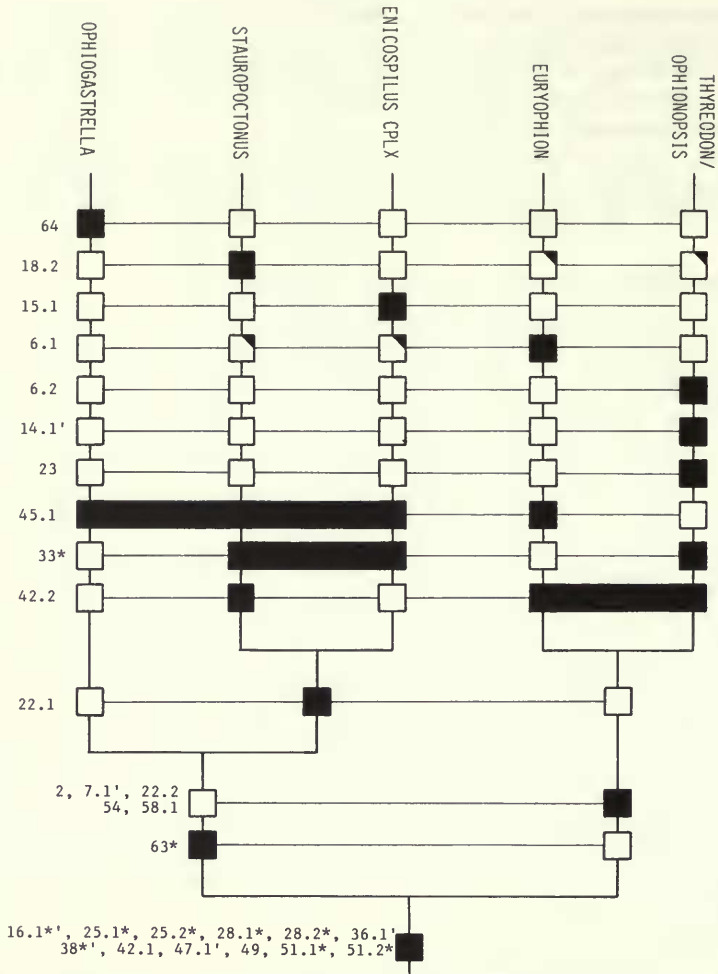


Fig. 20 Putative phylogenetic inter-relationships between groups of taxa in the *Enicospilus/Stauropectonus* and *Thyreodon/Euryophion* complexes.

number of characters have been labelled highly for certain taxa; this will be discussed below.

Wagner analysis of this data set yielded a number of equally short cladograms with quite different topologies (Figs 21–24). A large number of other trees that were only slightly less parsimonious were also generated (Gauld, unpublished data). Compatibility analysis yielded a single largest clique of 11 informative characters (2, 3, 7.1, 17, 25.1, 26, 38, 40, 41, 47.1 and 52.1) which supports the cladogram shown in Fig. 25. Although differing in many topological details, certain features are common to the dendrograms. In all of the Wagner trees the two major complexes emerged as the most derived groups. Five taxa (938, 939, 941, 948 and 951) occupy the most primitive position in three of the dendrograms and are amongst the eight most primitive taxa in the other two, suggesting these species are amongst the most primitive of all ophionines. This group of species comprises examples of the genera *Xylophion*, *Ophion*, *Agathophiona*, *Rhopalophion* and *Sclerophion*. Gauld (1979) suggested these might represent a holophyletic group, the *Ophion* subgroup, characterized by having a slender *Rs+2r*, which is also straight basally, having an incomplete posterior transverse carina of the mesosternum, having a subapically impressed clypeus, having *1m-cu* usually with a ramellus, and always angled, and having the anterior area of the propodeum 'occluded'. However, the holophyly of the group is open to question. The shape of *Rs+2r* (corresponding to characters 39, 40 and 62), of *1m-cu* (38

Table 17 Results of LeQuesne test on data set comprising HTUs and unplaced taxa (905, 906, 920, 922, 923, 927, 938, 939, 940, 941, 948, 949, 950 and 951). Conventions as in Table 2.

| Character number: | | incompatibilities observed | expected | O/E ratio | | | | | | | | | | | |
|-------------------|----|----------------------------|----------|---------------|----|------|------|---------------|----|------|------|---------------|----|------|------|
| <u>1.1</u> : | 44 | 45.4 | 0.97 | <u>1.2</u> : | 38 | 37.7 | 1.01 | <u>2</u> : | 15 | 25.6 | 0.59 | <u>3</u> : | 26 | 38.2 | 0.68 |
| <u>5.1</u> : | 35 | 38.2 | 0.92 | <u>6.1</u> : | 30 | 38.2 | 0.79 | <u>7.1</u> : | 35 | 37.4 | 0.94 | <u>7.2</u> : | 47 | 61.0 | 0.77 |
| <u>9</u> : | 35 | 38.2 | 0.92 | <u>12</u> : | 36 | 38.2 | 0.94 | <u>14.1</u> : | 50 | 45.1 | 1.11 | <u>14.2</u> : | 46 | 54.1 | 0.85 |
| <u>15.1</u> : | 53 | 58.9 | 0.90 | <u>15.2</u> : | 30 | 37.5 | 0.80 | <u>16.2</u> : | 56 | 57.6 | 0.97 | <u>17</u> : | 24 | 25.6 | 0.94 |
| <u>18.1</u> : | 54 | 60.2 | 0.90 | <u>18.2</u> : | 35 | 37.4 | 0.94 | <u>19</u> : | 30 | 38.2 | 0.79 | <u>20.1</u> : | 60 | 60.0 | 1.00 |
| <u>20.2</u> : | 53 | 58.6 | 0.90 | <u>22.1</u> : | 45 | 60.0 | 0.75 | <u>22.2</u> : | 49 | 50.1 | 0.98 | <u>23</u> : | 43 | 51.1 | 0.84 |
| <u>24.1</u> : | 54 | 60.8 | 0.89 | <u>24.2</u> : | 44 | 50.1 | 0.88 | <u>25.1</u> : | 14 | 25.1 | 0.56 | <u>25.2</u> : | 58 | 61.2 | 0.95 |
| <u>26</u> : | 24 | 25.6 | 0.94 | <u>27.1</u> : | 53 | 58.6 | 0.90 | <u>27.2</u> : | 57 | 61.0 | 0.93 | <u>28.2</u> : | 57 | 59.6 | 0.96 |
| <u>29.1</u> : | 37 | 37.5 | 0.99 | <u>29.2</u> : | 52 | 58.9 | 0.88 | <u>30</u> : | 42 | 38.2 | 1.10 | <u>31</u> : | 28 | 25.6 | 1.09 |
| <u>32</u> : | 45 | 45.9 | 0.98 | <u>33</u> : | 50 | 60.9 | 0.82 | <u>35</u> : | 47 | 45.9 | 1.02 | <u>36.1</u> : | 25 | 24.9 | 1.00 |
| <u>36.2</u> : | 59 | 56.5 | 1.05 | <u>36.3</u> : | 28 | 37.3 | 0.75 | <u>37</u> : | 53 | 60.9 | 0.87 | <u>38</u> : | 34 | 51.1 | 0.67 |
| <u>39</u> : | 61 | 59.6 | 1.02 | <u>40</u> : | 22 | 38.2 | 0.58 | <u>41</u> : | 44 | 45.9 | 0.96 | <u>42.1</u> : | 61 | 60.2 | 1.01 |
| <u>42.2</u> : | 37 | 37.4 | 0.99 | <u>43.1</u> : | 44 | 37.4 | 1.18 | <u>43.2</u> : | 53 | 60.2 | 0.88 | <u>44.1</u> : | 59 | 61.2 | 0.96 |
| <u>44.2</u> : | 34 | 37.4 | 0.91 | <u>45.1</u> : | 48 | 45.0 | 1.07 | <u>45.2</u> : | 47 | 58.7 | 0.80 | <u>46</u> : | 33 | 45.9 | 0.72 |
| <u>47.1</u> : | 22 | 45.4 | 0.48 | <u>47.2</u> : | 34 | 37.7 | 0.90 | <u>48.1</u> : | 59 | 56.9 | 1.04 | <u>48.2</u> : | 32 | 37.5 | 0.85 |
| <u>51.1</u> : | 57 | 58.6 | 0.97 | <u>51.2</u> : | 55 | 60.7 | 0.91 | <u>52.1</u> : | 22 | 25.6 | 0.86 | <u>54</u> : | 39 | 45.9 | 0.85 |
| <u>55</u> : | 20 | 25.6 | 0.78 | <u>57</u> : | 56 | 59.6 | 0.94 | <u>58.1</u> : | 42 | 51.1 | 0.82 | <u>59</u> : | 45 | 59.6 | 0.76 |
| <u>61.1</u> : | 51 | 58.7 | 0.87 | <u>61.2</u> : | 41 | 45.0 | 0.91 | <u>62</u> : | 56 | 57.6 | 0.97 | <u>63</u> : | 52 | 60.9 | 0.85 |

Grand total- 1528 observed, 1705.7 expected. Overall O/E ratio = 0.90

Ranking ratios of scoring characters

| | | | | | | | | | | | | | | | | | | | | |
|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|----|------|------|
| 47.1 | 25.1 | 40 | 2 | 38 | 3 | 46 | 22.1 | 36.3 | 59 | 7.2 | 55 | 6.1 | 19 | 45.2 | 15.2 | 33 | 58.1 | 23 | 54 | 14.2 |
| 48.2 | 63 | 52.1 | 61.1 | 37 | 24.2 | 43.2 | 29.2 | 24.1 | 18.1 | 15.1 | 47.2 | 20.2 | 27.1 | 51.2 | 44.2 | 61.2 | | | | |
| 5.1 | 9 | 27.2 | 18.2 | 7.1 | 17 | 26 | 57 | 12 | 25.2 | 28.2 | 41 | 44.1 | 1.1 | 16.2 | 62 | 51.1 | 22.2 | 32 | 29.1 | |
| 42.2 | 20.1 | 36.1 | 1.2 | 42.1 | 39 | 35 | 48.1 | 36.2 | 45.1 | 31 | 30 | 14.1 | 43.1 | | | | | | | |

and 47) and the form of the propodeum (22) are symplesiomorphies and therefore not admissible for defining a holophyletic group. Both the incomplete posterior transverse carina of the mesosternum (equivalent to 1 scores for 27.1 and 27.2) and the impressed clypeus (corresponding to a 1 score for character 7.2) are apomorphic features found in many other taxa. In many of the Wagner trees generated the five taxa formed a clade defined by characters 18.1 and 44.1 in addition to 7.2 and 27.2 (27.1 is most parsimoniously considered an apomorphy of the subfamily). All of these characters are highly homoplastic so it is not surprising that the compatibility cladogram leaves these taxa as an almost unresolved paraphyletic assemblage.

Four further taxa, 920 (*Riekophion emandibulator*), 922 (*Sicophion pleuralis*), 940 (*Eremotylus boguschi*) and 950 (*Hellwigiella nigripennis*) have been placed in the same group as the *Ophion* subgroup (Townes, 1971; Gauld, 1979). The undescribed genus (949) would, on Townes' (1971) criteria, also belong to this group. There is no evidence in any analysis that suggests that these taxa and the *Ophion* subgroup constitute a holophyletic clade. The definition of the group as adopted by previous authors rests on a plesiomorphic feature, possession of a membranous flange on the fore tibial spur, suggesting this 'group' is in fact a paraphyletic assemblage. In Wagner analyses 920, 922, 940, 949 and 950 may be positioned primitively with respect to most other taxa (e.g. Figs 22, 24) but some members may occasionally be united with other taxa. Taxa 949 and 950 are sometimes placed in much more derived positions, the former within the *Enicospilus/Stauropoctonus* complex (e.g. Fig. 23) and the latter as the sister-lineage to the *Thyreodon/Euryophion* complex (e.g. Fig. 21). *Hellwigiella* (950) is placed as the sister-group to the *Thyreodon/Euryophion* complex on the basis of a number of shared, rather striking, derived characters. These characters (which may be shared by several or all species in the complex) are adaptations to a diurnal eremic existence, and include possession of small ocelli (12), a shorter stouter flagellum (14.1), pendant epipleuron 2 (30), cylindrical hind tibial spurs (54) and long weakly curved claws (58.1). Many or all of these features are also found in the

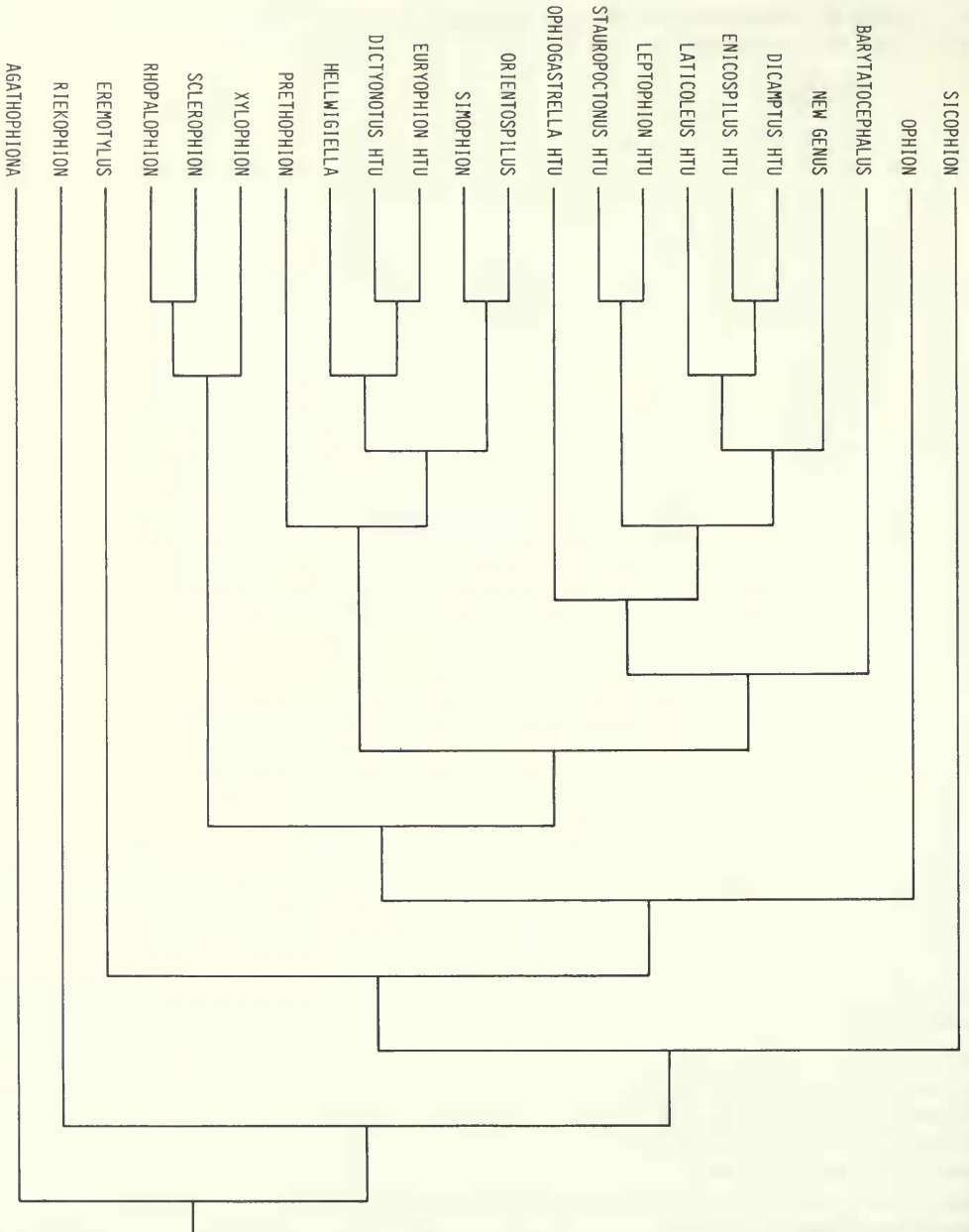


Fig. 21 283 transformation step cladogram derived from Wagner analysis of HTUs plus unplaced taxa.

apomorphic condition in other diurnal eremic ophionines including an undescribed species of *Ophion* from Australia (in ANIC) and *Agathophiona* species from Mexico. In another group of ichneumonids, the Anomaloninae, similar differences occur between closely related eremic and non-eremic organisms (e.g. *Gravenhorstia* (*Erigorgus*) and *Gravenhorstia* (*Gravenhorstia*) species (Gauld, 1976)). The occurrence of so many apomorphic states of these characters together in day-flying species strongly suggests the characters should be considered as a character suite and perhaps accorded less taxonomic weight. Unlike members of the *Thyreodon*/*Euryophion* complex, *Hellwigiella* shows the plesiomorphic state of important characters used for defining the group (2, 7·1, 44·2). Furthermore, a position near to the base of the common

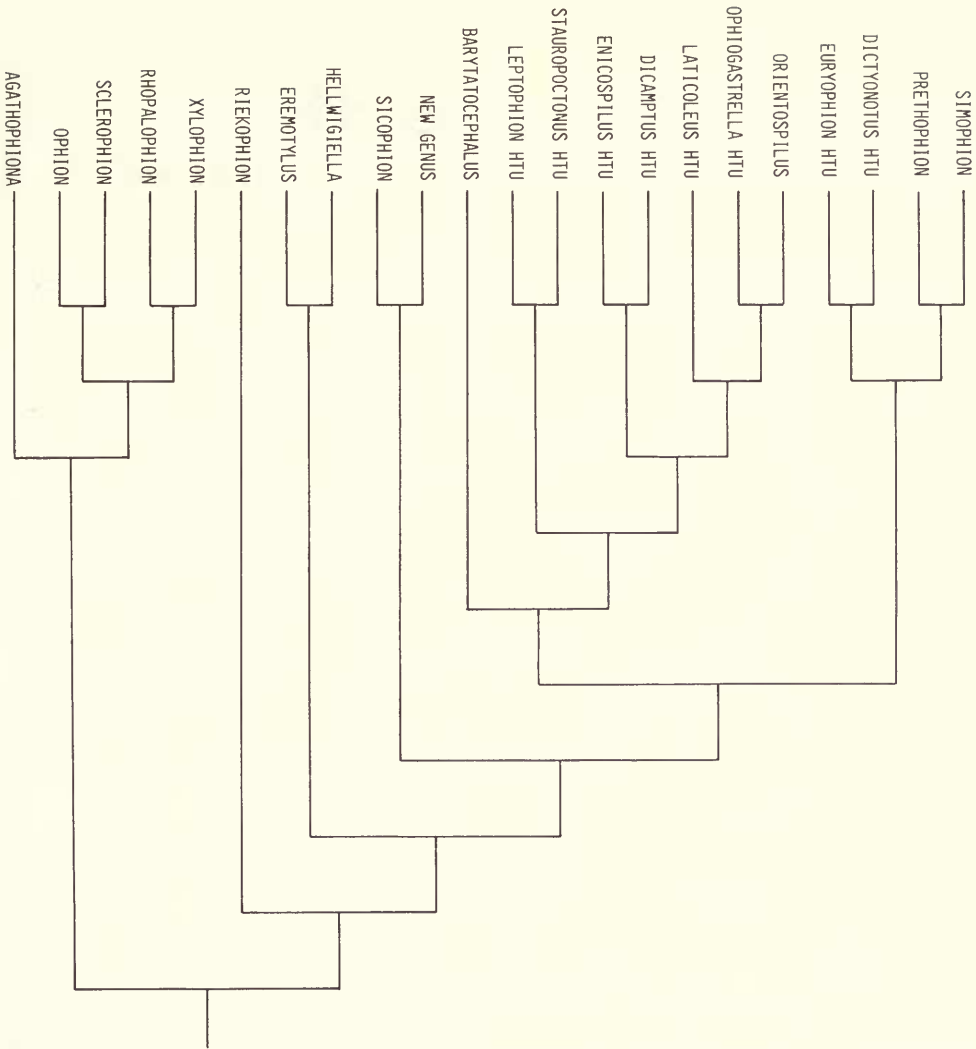


Fig. 22 283 transformation step cladogram derived from Wagner analysis of HTUs plus unplaced taxa.

stem of the two major complexes is suggested by the fact that *Hellwigiella* shows the plesiomorphic states of characters 16·1, 42·1, 52·1 and 52·2.

The position of the new genus (949) is rather perplexing as the taxon exhibits a number of derived features shared with the more specialized taxa, especially those in the *Enicospilus/Stauropoctonus* complex (e.g. 15·1, 16·1, 22·1, 33, 45·1) yet at the same time lacks one major apomorphy of the group (63). Taxon 949 also shows the plesiomorphic state of many of the stem characters, including 25·2, 28·2, 42·1, 51·1 and 52·2. It does, however, share a small number of derived features (including 1·1, 15·1, 16·1, 33 and 45·1) with another enigmatic taxon, *Sicophion pleuralis* (922). *Sicophion*, like taxon 949, is primitive in a surprising array of other features and it seems plausible that these two taxa have a sister-group relationship and represent a primitive group that evolutionarily converged with the *Enicospilus* group, possibly as a result of similar selection pressures. The striking phenetic resemblance between 949 and some species of *Leptophion* is perhaps more understandable when one considers these taxa have apparently evolved in mid altitude tropical cloud forests – 949 in the Neotropics and *Leptophion* in South East Asia.

Taxon 920, *Riekophion emandibulator*, is often placed with 967 and 968 (*Dicamptus* and

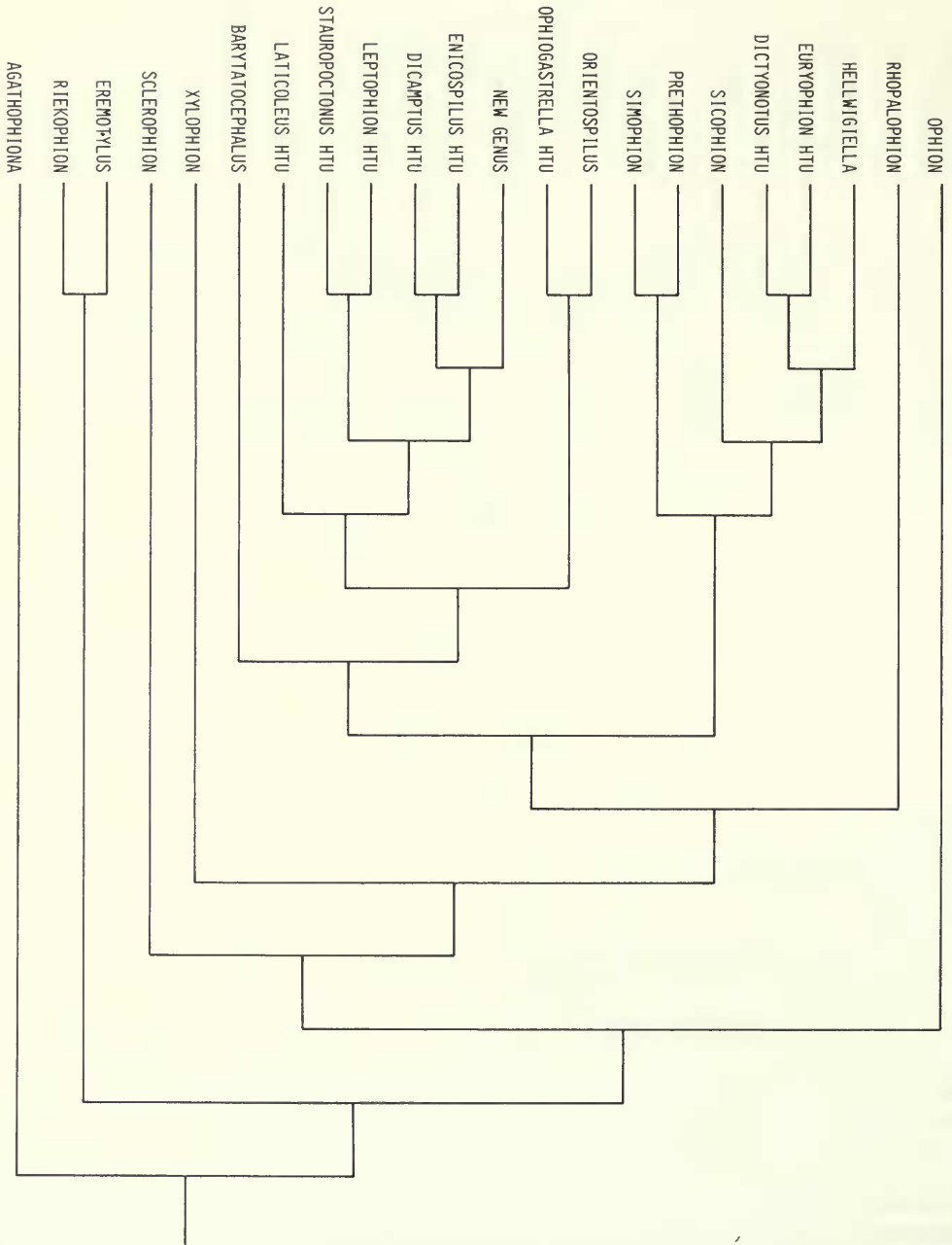


Fig. 23 284 transformation step cladogram derived from Wagner analysis of HTUs plus unplaced taxa.

Enicospilus) in compatibility analyses on the basis of sharing the derived states of characters 40 and 46 (e.g. Fig. 25). In other respects *Riekophion* does not appear to be at all closely related to either *Dicamptus* or *Enicospilus* (Gauld, 1977) and the high label scores obtained by the species for the derived states of these characters (Appendix 8) strongly suggests parallel derivation in two lineages.

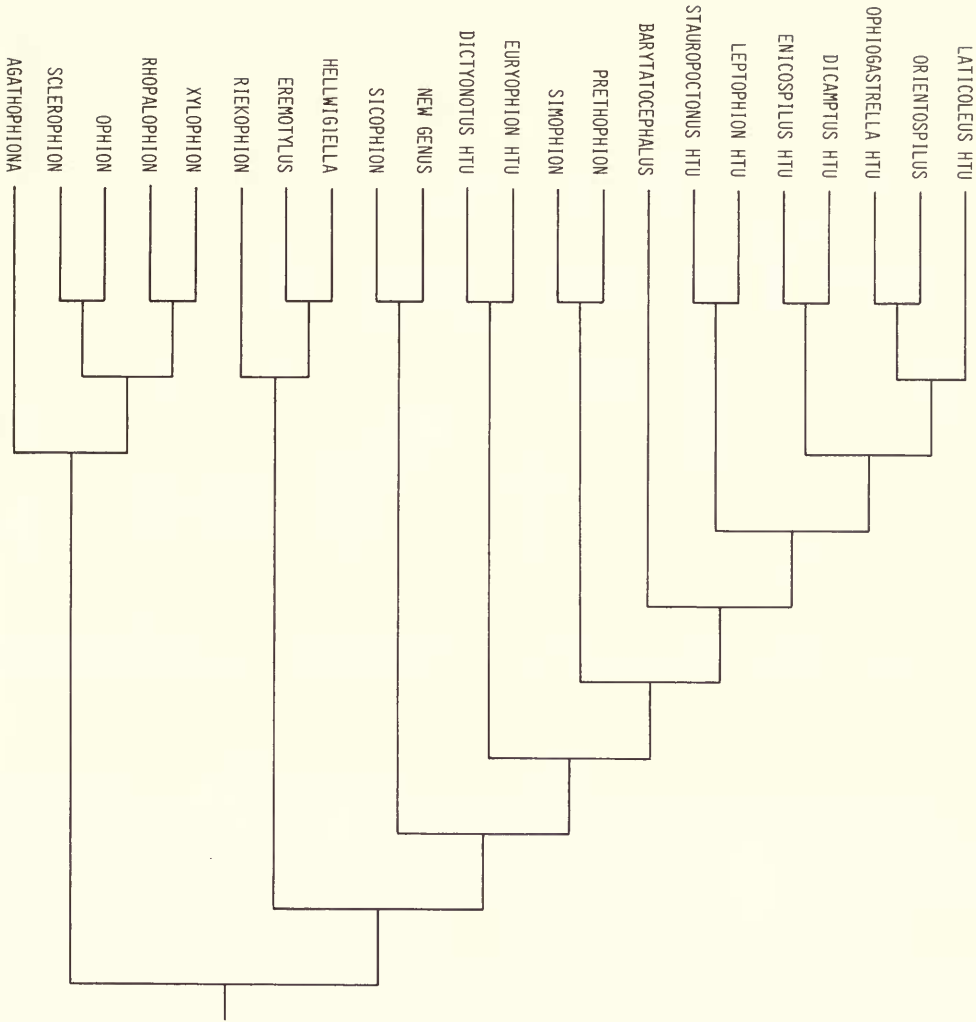


Fig. 24 284 transformation step cladogram derived from Wagner analysis of HTUs plus unplaced taxa.

Accepting that the taxa of the *Ophion* 'genus group' (920, 922, 938–41, 948–51) are the most primitive ophionines, then the most parsimonious arrangement of these taxa with respect to all other groups is that presented in Fig. 26. All other ophionine taxa, 922 + 949 + 920 and 950 + 940 remain as an unresolved trichotomy. The *Ophion* genus-group (i.e. the Ophionini of Townes, 1971) is therefore a paraphyletic grade, an assemblage of less-specialized ophionines. The 'group' possibly comprises three apparently holophyletic clades, the *Ophion*-group (= *Ophion* subgroup of Gauld, 1979), the *Eremotylus* group (940, 950) and the *Sicophion* group (920, 922, 949). The clade, 'all other ophionine taxa', comprises the two groups discussed above (the *Thyreodon*/*Euryophion* complex and the *Enicospilus*/*Stauropoctonus* complex) and four unplaced taxa, 905, 906, 923 and 927. The position of these four taxa can now be considered in relation to the fairly rigid structure derived above.

Taxa 905 and 906 (*Simophion calvus* and *Orientospilus melasma*) share 27 derived characters (Appendix 3); 906 also has a large number in common with other taxa, particularly 947 (28), 946

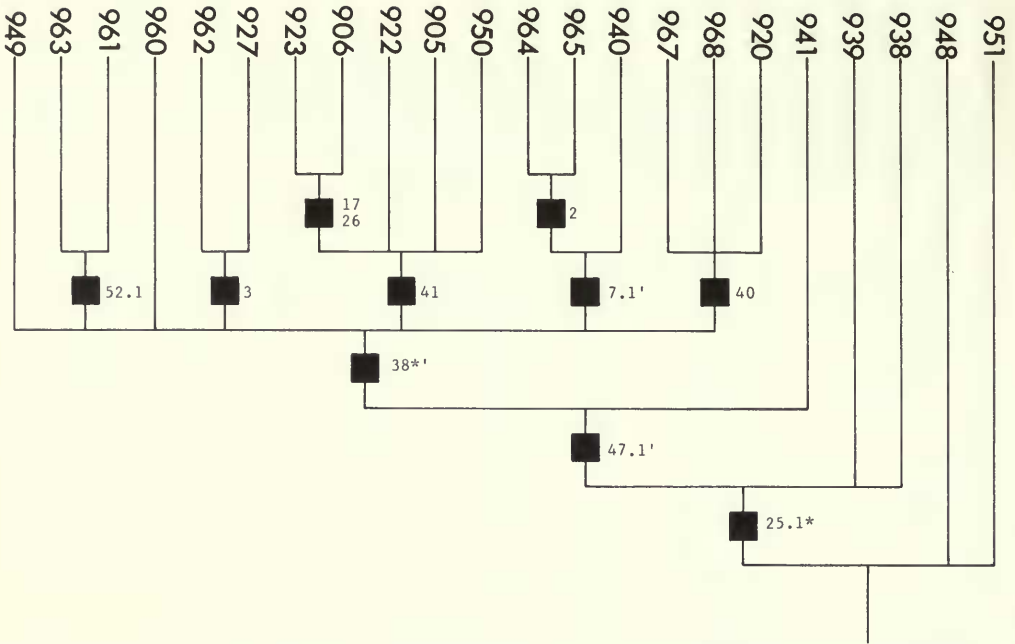


Fig. 25 Cladogram based on largest compatible set of characters obtained from HTUs plus unplaced taxa.

(27), 942 (26), 918, 915, 914, 911 and 910 (25). Taxon 905 is less closely associated with other taxa but shows some affinity with the *Euryophion* group (937 (25), 936 (24) and 935 (23)). Taxa 905 and 906 share several unusual apomorphic features including 6·1 (elsewhere only found in the derived state in 909, 935–37 and 946), 19 (elsewhere only found in 908, 918, 935 and 937), 23 (elsewhere only found in the *Dictyonotus/Thyreodon* lineage) and 41 (elsewhere only found in 922 and 923). Taxa 905 and 906 also share all the stem characters of the *Enicospilus/Stauropogon* + *Thyreodon/Euryophion* lineage, except that 905 is plesiomorphic for 42·1. This suggests that they may belong near the other groups, possibly as a sister-species pair. Of the features defining the two major complexes these taxa share only one, an apomorphy of 63, suggesting placement near the base of the *Enicospilus/Stauropogon* lineage. It is noteworthy that in earlier Wagner analyses (e.g. Figs 22–24) 905 and 906 generally were split up, 905 often grouping with 923, 964 or 965, whilst 906 usually was united with 960 or 961. If the two taxa were entered together first in the data file, then they were not separated, but remained as a distinct clade (Fig. 21).

Taxon 927 (*Baryatocephalus mocsaryi*) shares 24 derived characters with taxon 936, 23 with 914 and 946 and 22 with 913. It shares all the stem features with the major complexes and additionally has the apomorphic condition for 22·2 and 58·1, suggesting it belongs near the base of the *Thyreodon/Euryophion* lineage. It does not have the major apomorphies of the *Enicospilus/Stauropogon* branch (that is 22·1, 33 and 63).

Taxon 923 (*Prethophion latus*) is an enigmatic Neotropical taxon that has relatively few characters in common with any other species. The largest number, 22, are shared with 918 and it has 21 in common with 906. It does have all the 'gain' stem apomorphies in common with other higher taxa, but is plesiomorphic for 25·2, 28·2 and 45. It does not have any of the apomorphies defining the *Thyreodon/Euryophion* complex, but is apomorphic for character 63, suggesting it belongs near the base of the *Enicospilus/Stauropogon* stem. It is most parsimonious to treat *Prethophion latus* as the sister species of the 905 + 906 lineage (on the basis of the derived state of characters 27·1 and 27·2), but this association must be regarded as very tenuous.

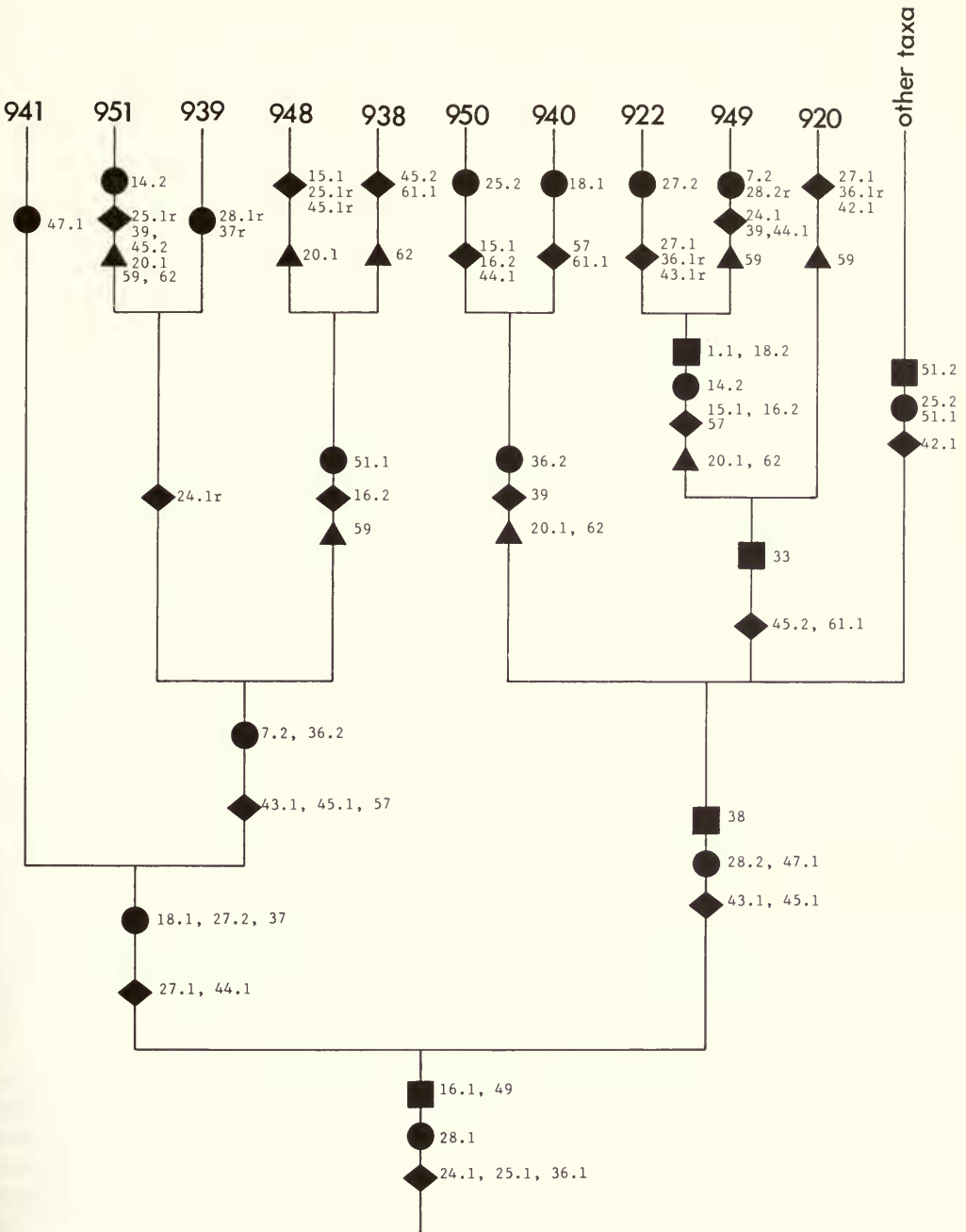


Fig. 26 Most parsimonious arrangement of 'Ophion genus-group' and all other taxa. Conventions as in Fig. 13.

The cladogram showing the preferred arrangement of taxa as described above is shown in Fig. 27. It is interesting to note that this user defined cladogram is one step more parsimonious than any obtained by Wagner analysis.

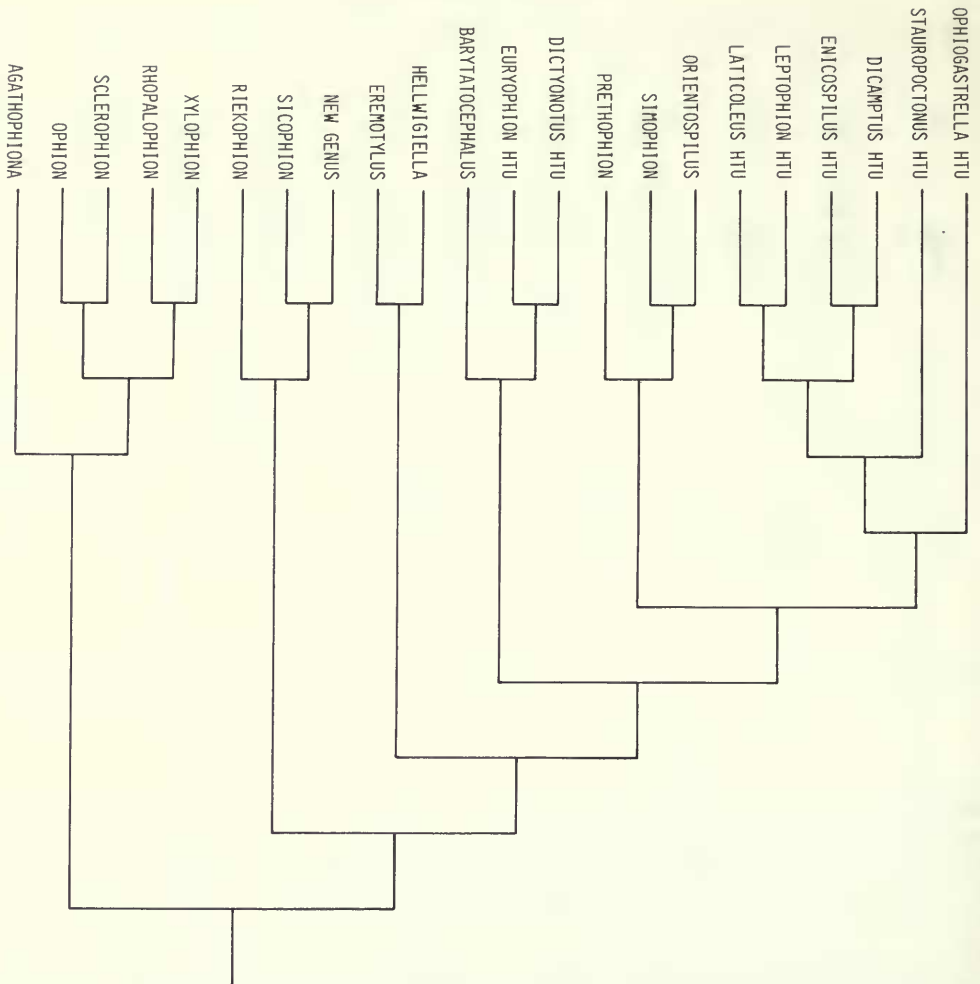


Fig. 27 Cladogram derived from subjective evaluation of character complexes involved in grouping taxa in cladograms presented in Figs 21–25. It is noteworthy that this, at 242 steps, is a more parsimonious arrangement than the best obtained by Wagner analysis, though this is a fortuitous event.

Discussion of suggested phylogeny

A putative phylogeny of the Ophioninae is shown in Fig. 27. Parts of this cladogram seem to be fairly robust, but other groups are only supported by weak homoplastic characters. The overall arrangement, placing the *Ophion* and *Eremotylus* groups in primitive positions and having a bifurcated evolutionary line, does seem reasonably sound. It corresponds with increasing morphological complexity, particularly in the form of the fore tibial spur (character 51), the region of the spiracular sclerite (character 15), the modification of the propodeum (characters 22, 25) and the loss of umbo (character 33). What little is known about the structure of the final instar larvae supports this arrangement. The cephalic capsules of the larvae of *Enicospilus*, *Dicamptus*, *Euryophion* and *Thyreodon* are clearly more specialized than those of *Ophion* in having a modified hypostoma (Short, 1978). The larvae of *Euryophion* and *Thyreodon* are similar in having numerous setae (11+) on each part of the maxillary lobe median to the hypostomal spur and adjoining the maxillary palp. *Dicamptus* and *Enicospilus* have eight or less setae in this position. Certain venational characters also support the phylogeny proposed. These include modification of *1m-cu* and broadening of the base of *Rs+2r* (characters 38, 47 and 62).

However, in almost all adult characters it is necessary to postulate parallelism. Reduction of the tibial spur membrane has occurred independently in *Xylophion* and the main evolutionary line, and specialization of the propodeum has occurred in both the main lineage and *Eremotylus*. It is quite disconcerting to see the degree of evolutionary convergence that has occurred in separate lineages (such as the development of alar sclerites and a sinuous *Rs+2r* in *Riekophion* and *Dicamptus/Enicospilus* and the general similarity of structure between the undescribed Costa Rican genus and species of *Leptophion*). No amount of rearrangement of lineages could possibly remove any but a small proportion of such homoplasy. Perhaps the development of such similarities is due to some underlying adaptation of the genotype not visually manifested (the underlying synapomorphies of Saether, 1979). It is difficult to explain otherwise (unless one postulates reticulate evolution – ‘ancient hybrids’ giving introgression) how such an unusual feature as alar sclerites has appeared, apparently independently in at least six evolutionary lineages of Ophioninae (*Afrophion*, *Sclerophion*, *Leptophion*, *Laticoleus*, *Riekophion* and *Dicamptus/Enicospilus*). Similar examples of such unusual parallelisms can be found in the modification of the penultimate distal hamulus, the projecting pecten of the hind tarsal claw and the development of a spine on the hind trochantelli.

The *Ophion* group of genera (*Ophion*, *Alophophion*, *Sclerophion*, *Afrophion*, *Rhopalophion*, *Agathophiona*, *Xylophion*) is defined by the possession of the apomorphic states of four rather homoplastic characters, the loss of the posterior transverse carina of the mesosternum (27·2), the possession of a diagonal mesopleural furrow (18·1), possession of an impressed clypeal margin (7·2) and having *Rs* in the hind wing at least slightly curved (44·1). Not all species of these genera necessarily possess all these apomorphies; *Afrophion* species are exceptional in having both a blunt clypeal margin and a straight *Rs* whilst some *Rhopalophion* species have the mesopleural furrow obsolescent. Although this genus-group is amongst the most primitive of ophionines, its position at the base of the phylogenetic tree rests on the assumptions that characters 38 and 47·1 (shape of *1m-cu* and presence of a ramellus) are correctly polarized. As mentioned above (pp. 77, 78) the polarity of both features is questionable and if it could be demonstrated that the assigned polarity is incorrect then these two features would become convincing apomorphies supporting the holophyly of the *Ophion* group. This change in polarity would necessitate placing the *Ophion* group a little higher up the evolutionary tree, possibly as the sister lineage to the *Eremotylus* group; these two groups share the apomorphic states of characters 18·1 and 44·1.

The holophyly of the *Eremotylus* group is supported by the angulate base of *Rs+2r* (39), which is somewhat thickened (62), and by the form of the clypeus. In most species it is slightly flared outwards in profile (7·1) and often slightly concave. The mandibles are a subtly different shape to those of virtually all other ophionines but this feature is very difficult to define.

The *Sicophion* group is a rather tenuous association of primitive taxa. The holophyly of the group is supported by the apomorphic states of characters 33 and 45·2. Apart from possession of certain primitive features such as the plesiomorphic state of character 51·2, and more extensive propodeal carination, all of these taxa appear to be highly specialized, sharing a variety of apomorphic features with other taxa placed higher up the phylogenetic tree. More evidence of the holophyly of this group needs to be obtained before it can confidently be accepted.

The holophyly of the *Thyreodon* group is supported by the specialized form of the anterior part of the propodeum (character 22·2) and by the form of the claw (character 58·1). The inclusion of *Barytatocephalus* within this clade does seem reasonable. In addition to the characters used in the analysis, two other features suggest *Barytatocephalus* belongs here. Vein *3r-m* in the fore wing of species of this genus forms a more obtuse angle with *Rs+2r* than is the case with most other ophionine taxa. Most other members of this clade have a similar specialization. At the base of the hind wing, in the anal cell, a vestige of a vein (? 2A) is often discernible. In most ophionines this trace, when observable, can be seen to be fairly near to and parallel with the hind margin of the wing; in both *Barytatocephalus* and other members of the *Thyreodon* complex (but not *Euryophion*) this vein trace is remote from the wing margin and close to and parallel with 1A. Townes (1971) considered *Barytatocephalus* to be a derivation of *Enicospilus*, but there is little evidence for this supposition. The exposed spiracular sclerite, the

general head shape and form of the propodeum suggest *Barytatocephalus* should not be included in the *Enicospilus* lineage.

The *Enicospilus* group is the largest complex and one of the most difficult to define. Its holophyly is supported by a single apomorphy, loss of vestigial first laterotergites (character 64), but the included taxa do resemble each other in possessing a large number of derived features in common. Within this group five subordinate lineages are recognizable, the *Orientospilus*, *Ophiogastrella*, *Stauropoctonus*, *Leptophion* and *Enicospilus* subgroups. Each of these is apparently a holophyletic group. These are the various groupings recognized in the classification proposed below.

A classification of the Ophioninae

Hennig (1966) pointed out the existence of two sorts of monophyletic taxa – holophyletic and paraphyletic groups. Traditional taxonomists may accord either group the status of a super-generic rank, though cladists do not recognize paraphyletic taxa (Farris, 1979; Carpenter, 1982). Whilst there are many cases of small paraphyletic taxa that can be satisfactorily amalgamated with a holophyletic taxon to form a slightly larger holophyletic taxon (e.g. *Aulophion* + *Stauropoctonus*), there are other cases where dogmatic adherence to cladistic tenets produces impractical results. For example, if the Hawaiian genera were incorporated into *Enicospilus* to give a single holophyletic taxon, the resultant genus would contain an extraordinary range of morphological and probably biological diversity. I concur with Martin (1981) in believing that a classification, as opposed to a phylogeny, is a compromise between known or hypothesized inter-relationships and nomenclatural convenience. A good classification has at least two important facets: (a) it facilitates generalizations to be made about the component taxa, and (b) it is predictive. Farris (1979) and Mickevich (1978) both contend that a purely phylogenetic classification is an optimum as it is both more predictive and more stable than one that is not entirely phylogenetic. Whilst I agree with these authors that this is *often* the case, I do not think it is always so, especially where there are very unequal rates of evolution in different lineages. Consider, for example, the ichneumonid subfamily Mesochorinae. Five genera, *Cidaphus*, *Astiphromma*, *Mesochorus*, *Stictopisthus* and *Plectochorus* each show progressive morphological complexity. All are quite large genera and are functionally useful, but only *Plectochorus* appears to be holophyletic. Each of the other four taxa is apparently paraphyletic with respect to the genera that are more specialized than it (Townes, 1971; Gauld, 1984b). Although not a strict phylogenetic classification, this arrangement of the species (which is based on adult morphological features) was found to have predictive value for larvae (see Short, 1978) which seem to corroborate the idea that these taxa are a nesting paraphyletic series. I personally see no way of establishing a strict phylogenetic classification for such a group, other than by lumping all the genera, an action that would result in a much less informative and less useful classification than the present one.

The existence of such nesting paraphyletic groups would seem to be a corollary of the punctuational model of evolution. Stanley (1979) argues convincingly that many major adaptive changes have occurred very rapidly in isolated populations – thus a new organizational level (higher taxon) may have arisen from a small population of a pre-existing (and, if the rate of phyletic evolution is small, virtually unchanging) species placed in a different higher taxon.

To return to the present example. If the Hawaiian genera have resulted from rapid radiation from an *Enicospilus* ancestor into niches hitherto, for enicospilines, unexploited, it is fairly unlikely that any prediction made from study of the biology of continental *Enicospilus* species will apply to *Pycnophion*. Similarly, any generalizations made about *Enicospilus* are likely to have to be prefaced by 'except in some Hawaiian species'. Consequently the purposes of prediction and generalization would both be better served by recognizing the Hawaiian taxa as distinct genera, even though *Enicospilus* thus becomes a paraphyletic taxon.

A second area of contention relevant to the present work concerns the reality and recognition of polythetic superspecific taxa. The currently recognized ophionine genera have been accepted initially as monophyletic groups, though in several instances it has been mentioned that a

number are polythetic (Cushman, 1947). Some authors (e.g. Løvtrup, 1973) tend to dismiss polythetic taxa as the product of unsatisfactory discrimination. Whilst I accept that this is an explanation, I dispute that it is the most obvious one. Most cladistic studies reveal that homoplasy is a common phenomenon. If a data set is highly homoplastic, then logically it follows that some phylogenetically 'real' clades will only be definable in a disjunct (*sensu* Hull, 1965) way. Imposing a monothetic classification on such groups would result in the erection of a multiplicity of new genera, many of which would be monobasic. The resultant classification will have little predictive value as a high proportion of new taxa are likely to necessitate new genera for their accommodation (Gauld & Mound, 1982).

The following classification is suggested for the subfamily Ophioninae. It is not strictly cladistic, as it recognizes some paraphyletic taxa; however it is a fair approximation of the presumed phylogeny. Formal tribes are not recognized, but these could be used for the various genus-groups. It should be noted that some very small genera were not incorporated in the cladistic analysis (these are denoted by an asterisk), but they were closely studied in an earlier work (Gauld, 1979). This has facilitated their placement in the present system.

Subfamily OPHIONINAE

Ophionidae Shuckard, 1840

Enicospilini Townes, 1971

OPHION genus-group

Ophion Fabricius, 1798

Alophophion Cushman, 1947*

Sclerophion Gauld, 1979 1980

Afrophion Gauld, 1979* 1980

Agathophion Westwood, 1882

Rhopalophion Seyrig, 1935

Xylophion Gauld, 1979 1980

SICOPHION genus-group

Riekophion Gauld, 1977

Sicophion Gauld, 1979

Janzophion gen. n.

EREMOTYLUS genus-group

Eremotylus Foerster, 1869

Trophophion Cushman, 1947*

Hellwigiella Szépligeti, 1905

THYREODON genus-group

Barytaocephalus Schulz, 1911

Euryophion Cameron, 1906

Rictophion Townes, 1971 *Syn. n.*

Dictyonotus Kriechbaumer, 1894

Ophionopsis Tosquinet, 1903

Syn. n.

Rhynchophion Enderlein, 1912

Thyreodon Brullé, 1846

ENICOSPILUS genus-group

Orientospilus subgroup

Prethophion Townes, 1971

Simophion Cushman, 1947

Orientospilus Morley, 1912

Ophiogastrella subgroup

Ophiogastrella Brues, 1912

Stauropactonus subgroup

Lepiscelus Townes, 1971

Stauropactonus Brauns, 1889

Aulophion Cushman, 1947 *Syn. n.*

Leptophion subgroup

Pamophion Gauld, 1977

Laticoleus Townes, *in* Townes & Townes, 1973

Leptophion Cameron, 1901

Enicospilus subgroup

Dicamptus Szépligeti, 1905

Enicospilus Stephens, 1835

Pycnophion Ashmead, 1900

Banchogastra Ashmead, 1900

Abanchogastra Perkins, 1902

Zoogeographic discussion

Present day distribution

The approximate numbers of species per area are given in Table 18. For the purposes of this discussion Melanesia, Australia and New Zealand are considered as a single region, the Australo-Pacific, whilst for purposes of comparison Hawaii, with three endemic and one cosmopolitan genera, is ignored.

Altogether 20 of the 32 ophionine genera (62.5%) are restricted to a single zoogeographic region. This is a surprisingly high proportion compared with many other ichneumonid subfamilies. For example, only about 30% of pimpline genera are endemic to a single region (Townes,

Table 18 Approximate numbers of species of various ophionine genera in each zoogeographic area.

| | PALAEARCTIC | AFROTROPICAL | ORIENTAL | MELANESIAN | AUSTRALIAN | NEW ZEALAND | HAWAIIAN | NEOTROPICAL | NEARCTIC |
|-------------------------|-------------|--------------|----------|------------|------------|-------------|----------|-------------|----------|
| <u>OPHION</u> | 50 | -- | 25 | 1 | 5 | 10 | -- | 30 | 50 |
| <u>ALOPHOPHION</u> | -- | -- | -- | -- | -- | -- | -- | 25 | -- |
| <u>SCLEROPHION</u> | -- | -- | 2 | -- | -- | -- | -- | -- | -- |
| <u>AFROPHION</u> | -- | 2 | -- | -- | -- | -- | -- | -- | -- |
| <u>AGATHOPHIONA</u> | -- | -- | -- | -- | -- | -- | -- | 1 | -- |
| <u>RHOPALOPHION</u> | -- | 3 | -- | -- | -- | -- | -- | -- | -- |
| <u>XYLOPHION</u> | -- | -- | -- | 1 | 3 | -- | -- | -- | -- |
| <u>RIEKOPHION</u> | -- | -- | -- | -- | 3 | -- | -- | -- | -- |
| <u>SICOPHION</u> | -- | -- | -- | -- | -- | -- | -- | 2 | -- |
| <u>JANZOPHION</u> | -- | -- | -- | -- | -- | -- | -- | 1 | -- |
| <u>EREMOTYLUS</u> | 8 | -- | 1 | -- | -- | -- | -- | 5 | 20 |
| <u>TROPHOPHION</u> | -- | -- | -- | -- | -- | -- | -- | -- | 1 |
| <u>HELLWIGIELLA</u> | 1 | -- | -- | -- | -- | -- | -- | -- | -- |
| <u>BARYTATOCEPHALUS</u> | 2 | -- | -- | -- | -- | -- | -- | -- | -- |
| <u>EURYOPHION</u> | -- | 7 | 1 | -- | -- | -- | -- | -- | -- |
| <u>DICTYONOTUS</u> | 1 | 2 | 2 | -- | -- | -- | -- | -- | -- |
| <u>RHYNCHOPHION</u> | -- | -- | -- | -- | -- | -- | -- | 3 | 1 |
| <u>THYREODON</u> | -- | -- | -- | -- | -- | -- | -- | 40 | 3 |
| <u>PRETHOPHION</u> | -- | -- | -- | -- | -- | -- | -- | 1 | -- |
| <u>SIMOPHION</u> | 2 | -- | -- | -- | -- | -- | -- | -- | 6 |
| <u>ORIENTOSPILUS</u> | -- | 2 | 1 | -- | -- | -- | -- | -- | -- |
| <u>OPHIOGASTRELLA</u> | -- | -- | -- | -- | -- | -- | -- | 11 | -- |
| <u>LEPISCELUS</u> | -- | 1 | -- | -- | -- | -- | -- | -- | -- |
| <u>STAUROPOCTONUS</u> | 1 | 1 | 2 | 1 | 1 | -- | -- | 4 | -- |
| <u>PAMOPHION</u> | -- | -- | -- | -- | 1 | -- | -- | -- | -- |
| <u>LATICOLEUS</u> | -- | 10 | -- | -- | -- | -- | -- | -- | -- |
| <u>LEPTOPHION</u> | -- | -- | 11 | 17 | 7 | -- | -- | -- | -- |
| <u>DICAMPTUS</u> | -- | 13 | 12 | 1 | 5 | -- | -- | -- | -- |
| <u>ENICOSPILUS</u> | 50 | 150 | 180 | 150 | 50 | 2 | 20 | 100 | 25 |
| <u>PYCNOPHION</u> | -- | -- | -- | -- | -- | -- | 3 | -- | -- |
| <u>ABANCHOGASTRA</u> | -- | -- | -- | -- | -- | -- | 1 | -- | -- |
| <u>BANCHOGASTRA</u> | -- | -- | -- | -- | -- | -- | 2 | -- | -- |

1969) and a similar proportion of genera of other subfamilies are likewise restricted. The majority of the restricted ophionine genera are small taxa with three or fewer species; only *Alophophon*, *Ophiogastrella* and *Laticoleus* are larger than this and they have ten or more species each.

Six of the more widely distributed genera occur in only two regions: *Rhynchophon* and *Thyreodon* (Neotropical/Nearctic), *Euryophon* and *Orientospilus* (Afrotropical/Oriental), *Leptophon* (Oriental/Australo-Pacific) and *Simophon* (Palaeartic/Nearctic). Two genera occur in just three regions, *Dictyonotus* (Palaeartic/Oriental/Afrotropical) and *Dicamptus* (Afrotropical/Oriental/Australo-Pacific), whilst *Eremotylus* occurs in four regions (Nearctic/Palaeartic/Oriental/Neotropic). *Ophion* occurs in all regions except the Afrotropical and *Stauropoctonus* in all but the Nearctic (though it is absent from the African mainland). Only *Enicospilus* is truly cosmopolitan with quite large numbers of species in all areas.

Considered from a geographical standpoint the Neotropical region contains both the most genera (12) and has the highest degree of generic endemism (50%). The Afrotropical and Oriental regions both contain ten genera, but the former has a far higher degree of endemism (40% compared with 10%). The Australo-Pacific region contains eight genera, three of which (37%) are endemic whilst the Palaearctic, with a similar number of genera, has only two endemics (25%). The Nearctic is the most impoverished with seven genera, one of which (14%) is endemic. The faunal similarity (at generic level) between the regions is shown in Table 19.

Table 19 The generic faunal affinities between major zoogeographic regions (Hawaii is excluded). The values at the intersects of rows and columns V may be defined as:

$$V = \frac{\text{number of genera common to areas X and Y}}{\text{total number of genera present in areas X and Y}}$$

It is noteworthy that contiguous or recently contiguous areas have a significantly higher value for V than do areas that are not contiguous or that have only been contiguous in the distant past (more than 40 million years ago), suggesting that dispersal may be a more important event than vicariance in the biogeographical history of the subfamily.

| | NEARCTIC | NEOTROPICAL | AUSTRALO-PACIFIC | ORIENTAL | AFROTROPICAL |
|------------------|----------|-------------|------------------|----------|--------------|
| PALAEARCTIC | 0.36 | 0.25 | 0.23 | 0.38 | 0.20 |
| AFROTROPICAL | 0.06 | 0.10 | 0.20 | 0.43 | |
| ORIENTAL | 0.21 | 0.22 | 0.38 | | |
| AUSTRALO-PACIFIC | 0.15 | 0.18 | | | |
| NEOTROPICAL | 0.36 | | | | |

Hypothesized evolutionary history of the group: a scenario

Primitive ichneumonids are known from the Upper Cretaceous (80–90mya) (Townes, 1973b) and the family may have originated at the beginning of the Cretaceous (Rodendorf & Rasnitsyn, 1980), possibly from a protoichneumonoid ancestor such as the Praeichneumonidae (Rasnitsyn, 1983). The age of the subfamily Ophioninae is not known but it is presumed that it post-dates the primitive Upper Cretaceous groups. A fossil *Ophion* species is known from the Lower Oligocene (35–40mya) in France and Rodendorf (1962) states that the Ophioninae (?sensu lato, i.e. including the Campopleginae) dates back to the Palaeocene (55–60mya). Possibly the group radiated around the beginning of the Tertiary some 65–70 million years ago.

At this time the continents were still in close proximity to one another (Audley-Charles *et al.*, 1981; Owen, 1981). Australia was connected to Antarctica and an archipelagic connection probably existed between this landmass and South America. Europe and North America were contiguous and South America was not widely separated from Africa. The most primitive lineage of the Ophioninae (the *Ophion* genus-group) may have been widespread at this time, as would have been its sister-group, the stem group of the remaining Ophioninae. The *Sicophion* lineage became isolated in the southern continent of Australia/Antarctica/South America at an early stage whilst its sister-lineage, the ancestor of the *Eremotylus*, *Enicospilus* and *Thyreodon* lineages, remained in Laurasia or Africa. The ancestor of the *Eremotylus* lineage probably differentiated in Laurasia whilst the ancestor of the *Enicospilus/Thyreodon* radiated in Africa. I suggest that early offshoots of this line must have spread to South America, either by flying

across the widening South Atlantic, or by dispersal through Laurasia and across a water gap to South America. Some kind of barrier to the spread of organisms to and from South America is suggested by the high degree of generic endemism and the fact that the Neotropical species of *Enicospilus* seem to belong to very few species-groups compared with those of other tropical areas. I suggest that the less vagile *Thyreodon* lineage reached South America much later, possibly from Asia via the Bering Straits. Probably the radiation of the *Enicospilus* lineage resulted in widespread extinction of members of the *Ophion* group, thus leaving the isolated specialized groups extant today. *Ophion* almost certainly has undergone secondary radiations giving rise to species complexes in South America (derived from the Nearctic) and Australia (derived initially from the Palaearctic fauna spreading through the Oriental region, where it has subsequently become isolated on mountain tops) (Gauld, 1984a). Except for *Xylophion*, a remnant of the early widespread *Ophion* group-distribution, and *Riekophion*, a remnant of the southern radiation of the *Sicophion* lineage, the ophionine fauna of the Australo-Pacific has largely been derived from the Oriental region (as has been observed for other groups, e.g. Wilson, 1959; Gupta, 1962), though New Guinea has served as the epicentre of a considerable radiation, particularly in the case of *Enicospilus*, over 100 endemic species of which occur on the island.

Although the above scenario is largely speculative it is the most parsimonious interpretation of the present distribution in relation to the postulated phylogenetic history of the group. Other scenarios would involve postulation of more widespread extinctions, more transoceanic dispersive events or necessitate postulating a much earlier origin for the subfamily.

The subfamily Ophioninae

In the following section the various genera and new synonymies are discussed in some detail. Keys have not been given here to genera as any attempt to produce a key to world genera would involve the usage of rather difficult couplets to allow for evolutionary parallelism between different species-groups in similar habitats in different zoogeographic regions. Practical keys to genera on a regional basis already exist. The Afrotropical region is covered by Gauld & Mitchell (1978) and the Indo-Australian region by Gauld & Mitchell (1981). This latter key will also suffice for the Palaearctic region. A key to the Neotropical genera is currently in preparation and this will suffice for the Nearctic. Townes (1971) also offers reasonable generic keys, but these are now rather dated, particularly his key to the 'Ophionini' (see Gauld, 1979).

The OPHION genus-group

This group contains seven genera, *Afrophion*, *Agathophiona*, *Alophophion*, *Xylophion*, *Sclerophion*, *Rhopalophion* and *Ophion*. The first six are holophyletic groups but *Ophion* is probably paraphyletic with respect to them (see p. 125).

The group is characterized by the absence of a posterior mesosternal transverse carina, usually by possession of a diagonal mesopleural furrow, generally by possession of an impressed clypeal apex and by having *Rs* in the hind wing usually at least slightly curved and often very strongly bowed. Virtually all species in this genus-group have *1m-cu* in the fore wing centrally angled somewhat, and usually have a distinct ramellus present at this point.

As *Ophion* is apparently the paraphyletic stem-group from within which all other genera in this group have arisen, and the genus is primarily a Holarctic taxon, it seems probable that this group originated in the temperate north. It is probable that at some period it was present in most regions and has gradually disappeared from equatorial regions leaving isolated relicts in South Africa (*Afrophion*), Australia (*Xylophion*), Madagascar (*Rhopalophion*) and Patagonia (*Alophophion*). The possibility that there has been repeated expansion into and extinction within the tropics is suggested by the presence of some groups of *Ophion* species on isolated mountains in South East Asia, New Guinea and South America, and by the occurrence of distinctive *Ophion* species-complexes in Australia and New Zealand (Gauld, 1984a).

AFROPHION Gauld

Afrophion Gauld, 1979: 79. Type-species: *Ophion nubicarpus* Tosquinet, by original designation.

Mandibles stout, not twisted, subequally bidentate, barely narrowed apically; outer mandibular surface convex, with strong proximal concavity. Maxillary palp 5-segmented, labial palp 4-segmented; clypeus in profile weakly convex with apical margin sharp but not clearly impressed; clypeus in anterior aspect weakly convex. Ocelli large, the posterior ones very close to the eyes; frontal carina absent; occipital carina complete, ventrally joining hypostomal carina. Antennae moderately long, 1.3 times length of fore wing. Pronotum unspecialized; spiracular sclerite exposed; notauli vestigial; epicnemial carina complete; mesopleural furrow strong, diagonal. Scutellum moderately convex, quite narrow and not carinate laterally; posterior transverse carina of mesosternum absent except laterally. Propodeum with anterior area either occluded or extremely short, the remainder of the propodeum rather abruptly declivous, with irregular vestiges of carinae and rather coarsely microreticulate. Fore wing with pterostigma broad; marginal cell elongate; $Rs+2r$ very broad and slightly angled before joining pterostigma; anterior corner of discosubmarginal cell glabrous, in one species extensively so and with a detached alar sclerite (Gauld & Mitchell, 1978); $1m-cu$ with small ramellus, centrally angled. Hind wing with Rs from straight to weakly curved. Fore tibial spur with a membranous flange behind macrotrichial comb; mid and hind trochantelli unspecialized; inner hind tibial spur flattened, with a margin of close fine hair; hind tarsal claws unspecialized, those of male slightly more closely pectinate than those of the female. Gaster slender; tergite 2 elongate, with thyridia very weak, close to anterior margin; umbo distinct; epipleuron up-turned. Ovipositor sheath slender; male with gonosquamae very large, ploughshare-like.

Afrophion is restricted to the extreme south of Africa. The genus contains two species, the type-species and *A. hynnisi* (Gauld & Mitchell). It is distinguished from *Ophion* by the form of the propodeum, the unique structure of the male genitalia and by the basally incrassate $Rs+2r$ in the fore wing.

AGATHOPHION Westwood

Agathophiona Westwood, 1882: 19. Type-species: *Agathophiona fulvicornis* Westwood, by monotypy.

Mandibles twisted 5–10°, barely tapered, with lower tooth slightly the longer; outer mandibular surface slightly convex, with a strong proximal concavity. Maxillary palp 5-segmented, labial palp 4-segmented; mouthparts exceptionally specialized in that the distal part of the maxilla projects below the clypeus and the labial glossae project by a distance almost equal to length of hind wing; clypeus in profile rather flat, margin blunt; clypeus in anterior aspect broad, very weakly convex. Ocelli quite small, the posterior ones separated from eye by about their own minimum diameter; frontal carina absent or present but weak; occipital carina dorsally complete or narrowly obsolescent centrally, ventrally obsolescent, not joining the very weak hypostomal carina. Antennae rather short and quite stout, distal segments quadrate. Pronotum unspecialized; spiracular sclerite exposed; notauli short but strongly impressed near anterior margin; epicnemial carina more or less complete; mesopleural furrow virtually absent. Scutellum moderately strongly convex, not laterally carinate; posterior transverse carina of mesosternum present only laterally as vestiges. Propodeum with anterior area occluded, rather deeply impressed; propodeal carinae vestigial; posterior area striate or coriaceous. Fore wing with pterostigma moderately broad; marginal cell slender; $Rs+2r$ more or less straight, not thickened before joining pterostigma; discosubmarginal cell without a glabrous anterior area; $1m-cu$ generally with only a trace of a ramellus, rather evenly but quite strongly curved. Hind wing with Rs quite strongly curved. Fore leg with tibial spur bearing a membranous flange behind the macrotrichial comb; mid and hind trochantelli unspecialized; inner hind tibial spur cylindrical, with scattered hairs marginally; hind tarsal claws long and weakly curved. Gaster rather stout; tergite 2 in profile only slightly longer than posteriorly deep; thyridia small and close to anterior margin; epipleuron up-turned. Female with subgenital plate enlarged, as long as tergite 2 and medially notched; ovipositor sheath unspecialized.

Agathophiona is a monobasic genus; the type-species occurs in Mexico. *A. fulvicornis* is diurnally active (Townes, 1971). Structurally this is one of the most specialized of all ophionine genera. The remarkable mouthparts are presumably an adaptation to feeding from certain types of flowers but the function of the rather unusually modified female terminalia is not known.

ALOPHOPHION Cushman

Alophophion Cushman, 1947: 439. Type-species: *Ophion chilensis* Spinola, by original designation.

Mandibles not twisted, weakly narrowed apically, subequally bidentate; outer mandibular surface flat, usually punctate and hirsute. Maxillary palp 5-segmented, labial palp 4-segmented; clypeus in profile weakly convex, margin often impressed, sometimes very narrowly so; clypeus in anterior aspect weakly convex. Ocelli generally large, the posterior ones close to the eyes; frontal carina absent; occipital carina absent. Antennae moderately to very long, at least 1.3 times length of fore wing. Pronotum unspecialized or mediodorsally somewhat flattened and quite long; spiracular sclerite exposed; notauli present on anterior part of mesoscutum; epicnemial carina generally strong; mesopleural furrow distinct, diagonal, extending from episternal scrobe to near subalar prominence. Scutellum very weakly convex, usually narrow and not carinate laterally; posterior transverse carina of mesosternum absent except for lateral vestiges. Propodeum with anterior area occluded, transverse and often lateromedian longitudinal carinae discernible, often almost complete; posterior area smooth or rugulose. Fore wing with pterostigma broad; marginal cell long; *Rs+2r* slender, curved near proximal 0.3 before joining pterostigma near centre; dicosubmarginal cell with glabrous area anterior; *1m-cu* generally centrally angled, sometimes with a short ramellus which is directed more anteriorly than that of *Ophion*. Hind wing with *Rs* curved. Fore tibial spur with a membranous flange behind macrotrichial comb; mid and hind trochantelli unspecialized; inner hind tibial spur flattened, with a margin of long close hairs; hind tarsal claws unspecialized. Gaster moderately slender; tergite 2 in profile elongate, thyridia oval, separated from anterior margin of tergite by its own length or less, umbo distinct; epipleuron up-turned. Ovipositor sheath narrow.

Alophophion is a moderately large genus that is restricted to South America. The majority of species occur in southern Chile and Patagonia. Cushman, when describing *Alophophion* as a distinct genus, commented that it barely warranted generic distinction from *Ophion*. Whilst it is undoubtedly very close to *Ophion*, the combination of characters exhibited by the group clearly separate it as a holophyletic lineage. This lineage is characterized by the following apomorphies: occipital carina entirely absent; *Rs+2r* joining pterostigma near centre; first subdiscal cell stouter than normal; ramellus, when present, directed more anteriorly than that of other ophionines.

OPHION Fabricius

Ophion Fabricius, 1798: 210, 235. Type-species: *Ichneumon luteus* L., by subsequent designation, Curtis, 1836: 600.

Paniscus Schrank, 1802: 316. Type-species: *Ichneumon luteus* L., by monotypy.

Psylonychia Szépligeti, 1905: 21. [Nomen nudum.]

Stenophthalmus Szépligeti, 1905: 23. Type-species: *Stenophthalmus algiricus* Szépligeti, by subsequent designation, Viereck, 1914: 137. [Homonym of *Stenophthalmus* Becker, 1903.]

Pachyprotoma Kohl, 1906: 223. Type-species: *Ophion (Pachyprotoma) capitatus* Kohl, by monotypy.

Australophion Morley, 1912: 4, 30. Type-species: *Ophion peregrinus* Smith, by monotypy.

Neophion Morley, 1912: 4, 30. Type-species: *Neophion crassus* Morley, by subsequent designation, Viereck, 1914: 100.

Apatophion Shestakov, 1926: 262. Type-species: *Apatophion mirsa* Shestakov, by original designation.

Platophion Hellén, 1926: 13. Type-species: *Platophion areolaris* Brauns, by subsequent designation, Cushman, 1947: 475.

Potophion Cushman, 1947: 476. Type-species: *Potophion caudatus* Cushman, by original designation.

Psylonychia Cushman, 1947: 476. [Unavailable name, proposed in synonymy.]

Apomesus Townes, 1971: 54. Type-species: *Apomesus longiceps* Townes, by original designation.

Mecetron Townes, 1971: 60. Type-species: *Stenophthalmus choaspese* Uchida, by original designation.

Mandibles not twisted, from very weakly to moderately narrowed distally, generally subequally bidentate or with upper tooth slightly the longer; outer mandibular surface more or less flat, except for basal concavity, moderately punctate. Maxillary palp 5-segmented, labial palp 4-segmented; clypeus in profile weakly to moderately convex, margin impressed, acute; clypeus in anterior aspect weakly convex, rarely truncate or even slightly concave. Ocelli usually large, the posterior ones separated from eyes by less than their own diameters; frontal carina absent; occipital carina usually complete dorsally, ventrally not reaching the hypostomal carina, rarely with occipital carina mediodorsally obsolescent, or in a few species with it entirely absent. Antennae generally of moderate length, in a few deserticolous species the flagellum short and with central segments quadrate. Pronotum unspecialized; spiracular sclerite usually completely exposed; notauli weak but discernible on anterior 0.2 of mesoscutum; epicnemial carina generally strong and well developed on mesopleuron; mesopleural furrow strongly impressed, extending diagonally from

episternal scrobe towards subalar prominence. Scutellum weakly to moderately convex, usually carinate only on anterior 0.2 or less, rarely with lateral longitudinal carinae complete to posterior margin; posterior transverse carina of mesosternum usually present only laterally as vestiges. Propodeum with anterior area occluded except for a small semicircular depression centrally; propodeal carina variously developed, at most with both transverse carinae and the lateromedian longitudinal carinae complete, enclosing an area superomedial, in the most exceptional cases with all carinae only vestigial; posterior area usually rather smooth. Fore wing with pterostigma moderately to very stout; marginal cell very long and slender; $Rs+2r$ usually virtually straight, slender, barely broadened before joining pterostigma, in some species evenly broadened to join pterostigma; discosubmarginal cell with glabrous area in anterior corner; $1m-cu$ usually with a well-developed ramellus, rarely with stub-like indication of this vein present; $1m-cu$ centrally strongly geniculate. Hind wing with Rs from weakly to very strongly curved. Fore tibial spur with membranous flange behind the macrotrichial comb; mid and hind trochantelli unspecialized; inner hind tibial spur flattened, with a margin of close long hairs; hind tarsal claws unspecialized, those of males usually more closely pectinate than those of the female. Gaster moderately slender; tergite 2 in profile moderately to strongly elongate, usually with thyridia large, close to anterior margin; umbo well developed; epipleuron up-turned. Ovipositor sheath usually slender, in one species-group exceptionally stout.

Ophion is a very large genus that is widely distributed throughout the world except for the Afrotropical region. In tropical South America and South East Asia few species occur and these are restricted to high altitudes (Gauld & Mitchell, 1981). *Ophion* as currently defined is almost certainly a paraphyletic assemblage; *Agathophiona*, *Rhopalophion*, *Sclerophion*, *Xylophion*, *Alophophion* and *Afrophion* are phenetically highly divergent (Gauld, 1979), holophyletic species-groups which have probably arisen from within *Ophion*. A number of other phenetically less divergent species-groups were included by Gauld (1979) within *Ophion*, but as the phylogenetic relationship of the taxa becomes better understood it will be necessary to erect a number of additional genera in order to establish a system of holophyletic taxa. Previous authors (e.g. Morley, 1912; Cushman, 1947; Townes, 1971) have attempted to remove other species-groups from *Ophion* and treat these as separate genera, but in each case the group removed has not been holophyletic as comparatively few of the subtropical and eremic *Ophion* species are known. Recent collecting has greatly increased our knowledge of these insects but more work needs to be undertaken before it is possible to fully resolve this genus. The major species-groups of *Ophion* are outlined below; all except the unsatisfactorily resolved *luteus*-group are holophyletic but I have avoided treating these groups as distinct genera until the *luteus* anathema can be resolved. As each of these groups appears to be defined by a series of unique apomorphies it is not possible to suggest their phylogenetic inter-relationship.

***Ophion peregrinus* species-group.** This species-group contains all the described New Zealand *Ophion* species (Townes *et al.*, 1961). Its monophyly is suggested by the possession of a mediodorsally lengthened pronotum, having $Rs+2r$ joining the pterostigma distal to the pterostigma base and having the longitudinal lateral carina of the propodeum with a raised ridge diverging towards the propodeal spiracle. In *O. peregrinus* this is only weakly developed but in other taxa this ridge is frequently very strong and continuous with the carina, and the front part of the carina is absent so the apparent carina curves anteriorly towards the spiracle where it terminates. *O. peregrinus* is apparently the most primitive taxon as it retains most of the propodeal carinae and has a strongly geniculate $1m-cu$; the other taxa have only a vestige of the anterior carina (the lateromedian and posterior transverse carina are lacking) and frequently have a reduced ramellus and more evenly curved $1m-cu$. Most also have a fairly straight Rs in the hind wing.

***O. bicarinatus* species-group.** This complex contains *O. bicarinatus* Cameron, *O. facetious* Gauld & Mitchell, *O. gerdius* Gauld & Mitchell, *O. horus* Gauld & Mitchell and all of the described Australian species (Gauld, 1977). The group is characterized by possession of a proximally broadened $Rs+2r$ which is slightly curved before reaching the pterostigma. The European species, *O. minutus*, may belong to this group. The five Australian species form a monophyletic subgroup characterized by the black interocellar area. In the Oriental region the species of the *bicarinatus* group are restricted to mountains in Sri Lanka, India, Burma, Malaysia, Taiwan and Sumatra. Their present fragmented distribution and their paraphyletic nature with respect to the Australian species-group suggests that this group was more widespread throughout the Indo-Australian region in the past, probably when the climate was cooler (Gauld, 1984a).

***O. cronus* species-group.** This monobasic group is restricted to montane New Guinea (Gauld & Mitchell, 1981). The group is characterized by having a very sparsely hirsute discosubmarginal cell and a very short $3r-m$. It does not appear to be closely related to any other Indo-Australian species.

- O. caudatus* species-group.** This group is characterized by the elongate head shape; the eyes are more oval than normal and the labium is specialized in having the prementum extended far beyond the insertion of the labial palps (Gauld & Mitchell, 1981). This group contains *O. caudatus* (Cushman), *O. silus* Gauld & Mitchell, *O. longiceps* (Townes), *O. ascus* Gauld & Mitchell, *O. sumptuous* Gauld & Mitchell, *O. mastrus* Gauld & Mitchell and an undescribed species from Sulawesi (BMNH). All these species occur in mountains in the Oriental region. An undescribed species from high altitude in Peru (TC) has a similarly modified head and like other members of the *O. caudatus* group it has large wings, elongate trochantelli and virtually obscured mesopleural punctures. This Neotropical species clearly seems to belong in this species-group, but it is possible that the apomorphies defining the group are a suite of characters facilitating existence at high altitude and that the Neotropical and Oriental lineages have undergone morphological convergence.
- O. areolaris* species-group.** This group is characterized by the loss of occipital carina, possession of a quadrate scutellum and a somewhat broadened ovipositor sheath, and by having a characteristic pattern of propodeal carina in which the area superomedia is more or less discernible, the posterior transverse carina is often complete and the anterior transverse carina is absent except centrally. This group contains *O. areolaris* Brauns, *O. ocellaris* Ulbricht and *O. fuscomaculatus* Cameron. The first two are western Palaearctic species whilst *O. fuscomaculatus* has an eastern Palaearctic range that extends into the higher mountains of the Oriental region.
- O. similis* species-group.** This group contains the Palaearctic species *O. similis* (Szépligeti), *O. mirsa* (Shestakov), *O. buchariensis* Meyer and two undescribed Nearctic species. All are stout insects with short, compact gasters, rather convex, irregularly sculptured propodea and somewhat shorter antennae than is usual for species of this genus. The ocelli and eyes are moderately small so the orbital-ocellar distance and the malar space are broader than is normal for *Ophion* species. All are apparently diurnally active and most are associated with dry areas.
- O. dentatus* species-group.** This group contains *O. dentatus* Smith, *O. turcomanicus* Szépligeti and *O. virus* Gauld & Mitchell. The group is characterized by possession of unusually long, fairly slender mandibles, having long, weakly curved claws and possessing numerous spines on hind tarsal segments 1–3. Species of this group are widely distributed throughout the eastern Palaearctic region, particularly Central Asia. Several also extend into the drier parts of the Indian subcontinent.
- O. luteus* species-group.** This large group contains all of the other described species of the genus from the Palaearctic, Nearctic and Neotropical regions. It is apparently a paraphyletic group and I can only define it in terms of plesiomorphic features (i.e. absence of apomorphic characters exhibited by other species-groups). With more study it may be possible to subdivide this group into several holophyletic species-complexes but little is yet known about either the eastern Palaearctic or the Nearctic species.

RHOPALOPHION Seyrig

Rhopalophion Seyrig, 1935: 49. Type-species: *Rhopalophion curvus* Seyrig (= *Ophion discinervus* Morley), by original designation.

Mandibles not twisted, weakly narrowed apically, more or less equally bidentate; outer mandibular surface slightly convex with distinct proximal concavity. Maxillary palp 5-segmented, labial palp 4-segmented; clypeus in profile weakly convex, margin slightly impressed and reflexed or sometimes almost blunt; clypeus in anterior aspect weakly convex or truncate. Ocelli moderately small to large, the posterior ones separated from the eyes by less than 0.8 times their own maximum diameter; frontal carina absent; occipital carina complete, joining hypostomal carina close to base of mandible. Antennae of moderate length, at least 1.2 times as long as fore wing. Pronotum unspecialized; spiracular sclerite exposed; notauli virtually absent; epicnemial carina present, extending onto pleuron; mesopleural furrow absent or very indistinct. Scutellum weakly to moderately convex, laterally carinate for its entire length; posterior transverse carina of mesosternum absent except for lateral vestiges. Propodeum with anterior area occluded; anterior and posterior transverse carinae usually complete, rarely with the former vestigial, very rarely all carinae absent; longitudinal carinae not developed; posterior area finely alutaceous to smooth. Fore wing with pterostigma moderately broad; marginal cell long; *Rs+2r* almost straight, not or only very slightly expanded before joining pterostigma; discosubmarginal cell anteriorly broadly glabrous from base of *Rs+2r* to ramellus; *1m-cu* very angulate, with an extremely long ramellus that reaches at least 0.6 of distance to *Rs&M*. Hind wing with *Rs* virtually straight or very weakly curved. Fore tibial spur with membranous flange behind macrotrichial comb reaching 0.5–0.7 of length of spur; mid and hind trochantelli unspecialized; inner hind tibial spur moderately flattened, with a fringe of long close hairs;

hind tarsal claws unspecialized, those of male far more closely and finely pectinate than those of the female. Gaster slender; tergite 2 in profile moderately long with thyridia oval and close to anterior margin; umbo quite well developed; epipleuron up-turned. Ovipositor sheath slender.

Rhopalophion is a small genus with three described species, *discinervus* which is widespread throughout the Afrotropical mainland, and *divergens* and *parallelus* which are restricted to Madagascar (Delobel, 1975). *R. divergens* and *R. parallelus* are apparently sister-species and constitute a clade defined by the following apomorphic features, possession of small ocelli, possession of subquadrate lower face and possession of a relatively long malar space. This clade is the sister-lineage to *R. discinervus* which is defined by possession of a very angulate *1m-cu* and a distally swollen ramellus (Gauld & Mitchell, 1978). The females of *discinervus* are unusual amongst ophionines in that the distal tarsal segment of the female has a lateral projection. This is similar to one found in a species of *Ophiogastrella* (Cushman, 1947). *Rhopalophion* species are easily distinguished from other taxa in the *Ophion* genus-group on account of their unique venation, total lack of propodeal longitudinal carinae and long fore tibial spur.

SCLEROPHION Gauld

Sclerophion Gauld, 1979: 77. Type-species: *Pleuroneurophion longicornis* Uchida, by original designation.

Mandibles stout, not twisted, barely narrowed apically; outer mandibular surface weakly convex. Maxillary palp 5-segmented, labial palp 4-segmented; clypeus in profile weakly convex, margin not impressed; clypeus in anterior aspect weakly convex. Ocelli large, the posterior ones separated from eyes by less than 0.2 of their minimum diameter; frontal carina absent; occipital carina complete, ventrally reaching hypostomal carina. Antennae very long and slender, more than 1.7 times length of fore wing. Pronotum unspecialized; spiracular sclerite exposed; notauli weak but discernible; epicnemial carina complete, strong; mesopleural furrow weak, diagonal, with upper end rather broad and shallow. Scutellum moderately convex, carinate laterally on at least its anterior 0.4; posterior transverse carina of mesosternum absent except as lateral vestige. Propodeum with anterior area occluded except medially where it is semicircular; anterior and posterior transverse carinae usually complete, other carinae weak; posterior area usually rather smooth. Fore wing with pterostigma moderately slender; marginal cell elongate; *Rs+2r* thickened and evenly curved before joining pterostigma; discosubmarginal cell with an extensive glabrous area anteriorly, the distal margin of this area with a thickened corneous mark; *1m-cu* with long ramellus, centrally geniculate. Hind wing with *Rs* very weakly curved. Fore tibial spur with a membranous flange behind macrotrichial comb; mid and hind trochantelli unspecialized; inner hind tibial spur flattened, with margin of close, long hairs; hind tarsal claws unspecialized. Gaster slender; tergite 2 very elongate, with thyridia elliptical, close to anterior margin; umbo well developed; epipleuron up-turned. Ovipositor sheath slender.

Sclerophion species may be recognized by their characteristic fore wing venation, particularly the thickened *Rs+2r* and the corneous mark in the discosubmarginal cell. The genus contains two species, the type-species and *S. uchidai* Gauld & Mitchell. These occur in the mountains at the eastern Palaearctic/Oriental interface (Gauld & Mitchell, 1981).

XYLOPHION Gauld

Xylophion Gauld, 1979: 77. Type-species: *Ophion xylyus* Gauld, by original designation.

Mandibles not twisted, weakly to moderately tapered, subequally bidentate; outer mandibular surface flat, punctate, with proximal concavity. Maxillary palp 5-segmented, labial palp 4-segmented; clypeus in profile convex, margin impressed, acute; clypeus in anterior aspect weakly convex. Ocelli large, the posterior ones separated from eyes by their own minimum diameter or less; frontal carina absent; occipital carina strong, ventrally often reaching hypostomal carina, sometimes ventrally obsolescent. Antennae of moderate length or long, usually at least 1.5 times length of fore wing. Pronotum more or less unspecialized, though one species has trace of a median transverse crest; spiracular sclerite exposed; notauli quite weak but usually distinct on anterior 0.2 of segment, rarely absent; epicnemial carina strong, reaching onto pleuron above level of lower corner of pronotum; mesopleural furrow weak, diagonal. Scutellum weakly convex, at most carinate laterally on anterior 0.2; posterior transverse carina of mesosternum present only laterally as vestiges. Propodeum with anterior area more or less occluded except centrally where it is discernible as a semicircular area; anterior transverse carina usually more or less complete, posterior transverse carina from present laterally as vestiges to almost complete; longitudinal carinae vestigial; posterior area rather smooth. Fore wing with pterostigma large and triangular; marginal cell long; *Rs+2r* evenly broadened and curved before joining pterostigma; discosubmarginal cell with a large glabrous area in anterior corner;

1m-cu with a short ramellus, centrally angulate. Hind wing with *Rs* strongly curved. Fore tibia with a membranous flange extending from 0.1–0.3 of its length behind macrotrichial comb; mid and hind trochantelli unspecialized; inner hind tibial spur flattened, with a margin of long, close hairs; hind tarsal claws of female unspecialized, of male unique in having a central gap between an inner and outer row of pectinal teeth. Gaster slender; tergite 2 in profile very elongate with thyridia elliptical, separated from anterior margin by its own length or less; umbo strongly developed; epipleuron up-turned. Ovipositor sheath slender.

Xylophion is a small genus restricted to the Australian tectonic plate. Three species, one of which is undescribed, occur in south-eastern Australia. One of these, *X. xylus*, also occurs more widely throughout Australia and has been found in the New Guinea highlands (Gauld, 1984a).

Xylophion is characterized by the venation, particularly the possession of a very short *3r-m*, and the reduced flange on the fore tibial spur. A particularly striking, and hitherto unrecognized, autapomorphy of the genus is the form of the male tarsal claw. Instead of having a sinuous row of pectinal teeth present (as is normal for ophionines), *Xylophion* males have a marked discontinuity in the centre of the row between the teeth on the inner and outer edges of the claw. In its least derived form only the central gap exists (*Xylophion* species 1, BMNH) but the other two species are specialized further in different ways. *X. ketus* has the inner and outer marginal rows extended laterally so that there is a central overlap between the two parallel ends of the rows of teeth. In *X. xylus* there is a less pronounced overlap but the distal portion of the claw is flattened and the terminal tooth reduced so the pectinal row forms a 'fence' around the distal end of the claw.

The *SICOPHION* genus-group

This group comprises three genera, *Sicophion* and *Janzophion* from montane tropical South America and *Riekophion* from Australia. The species in this complex exhibit an unusual combination of plesiomorphic and apomorphic features. All possess a well-developed membranous flange on the fore tibial spur though none has an umbo on tergite 2 and often the upper corner of the pronotum is expanded to partially occlude the spiracular sclerite. It is suggested here that these three genera comprise a distinct lineage which is derived with respect to the *Ophion* group, and that the *Sicophion* group represents a separate southern radiation of the ophionines. However, as mentioned above (see p. 117), if the polarity of characters 38 and 47-1 has been misinterpreted then the *Ophion* lineage may represent a more derived group than the *Sicophion* lineage. If this were the case then it is possible that the *Sicophion* group is a collection of relict genera whose present southern distribution can be explained by Darlington's (1965) 'glove hypothesis'.

JANZOPHION gen. n.

Type-species: *Janzophion nebosus* sp. n.

Mandibles twisted perhaps 5°, slightly tapered distally, with upper tooth slightly the longer; outer mandibular surface with a diagonal line of hair extending from upper proximal corner to near centre. Maxillary palp 5-segmented, labial palp 4-segmented; clypeus in profile convex, margin impressed, in anterior aspect with margin weakly convex. Ocelli very large, the hind ones more or less contiguous with eyes; frontal carina absent; occipital carina absent. Antennae very long and slender, about 1.5 times length of fore wing. Pronotum unspecialized; spiracular sclerite partially concealed; notauli vestigial; epicnemial carina present laterally and ventrally; mesopleural furrow indistinct. Scutellum weakly convex, laterally carinate only on anterior 0.1–0.3; posterior transverse carina of mesosternum complete. Propodeum with anterior area long; anterior transverse carina and usually posterior transverse carina complete, often with a median longitudinal carina present; propodeum otherwise rather smooth. Fore wing with pterostigma moderately broad; marginal cell very long; *Rs+2r* bowed, thickened before joining pterostigma; discosubmarginal cell with glabrous area near anterior corner, but anterior to this is narrow hirsute region; *1m-cu* without a ramellus, proximally fairly straight, distally strongly bowed. Hind wing with *Rs* weakly curved; marginal cell proximally glabrous; penultimate distal hamulus longer than its fellows, the distal one slightly shorter but longer than the proximal ones. Fore tibial spur with a membranous flange behind the macrotrichial comb; mid and hind trochantelli unspecialized; inner hind tibial spur flattened, with margin of close long hairs; hind tarsal claw unspecialized. Gaster slender; tergite 2 in profile very elongate, with thyridia remote from anterior margin; umbo vestigial; epipleuron up-turned. Ovipositor sheath slender.

Janzophion is a distinctive genus which bears a very strong phenetic similarity to the Old World genus *Leptophion*. Unlike *Leptophion*, *Janzophion* species lack the occipital carina, and have a well-developed membranous flange present on the fore tibial spur, behind the macrotrichial comb.

***Janzophion nebosus* sp. n.**

Fore wing length 14–16 mm.

Head slightly more elongate than normal for ophionines; lower face polished, 1.4–1.5 times as long as broad; malar space 0.50–0.55 times basal mandibular width; head strongly narrowed behind eyes, occiput mediodorsally slightly concave. Flagellum with 66–68 segments, the tenth segment about 2.0 times as long as wide. Mesoscutum with margin slightly out-turned; scutellum finely shagreened; mesopleuron with upper part highly polished, finely and sparsely punctate, ventrally slightly more coriaceous; metapleuron similar. Propodeum in profile evenly declivous; propodeal spiracle joined to pleural carina by weak ridge; most of alitrunk bearing fine pale pubescence. Fore wing with $AI = 1.20\text{--}1.25$; $CI = 0.43\text{--}0.47$; $ICI = 0.61\text{--}0.70$; $SDI = 1.14\text{--}1.17$; *cu-a* proximal to base of *Rs&M* by about 0.3 times its own length; outer hind corner of 2nd discal cell about 90°. Hind wing with about 8 distal hamuli; $NI = 3.70\text{--}4.60$. Legs unspecialized; hind tarsal claws of male with slightly finer and denser pectinate comb than that of female. Gaster slender, male with subgenital plate bearing long fine pubescence; gonosquamae quite long, dorsally somewhat membranous.

Pale yellowish species, with interocellar area, part of mesoscutum, much of mesopleuron, metapleuron and part of propodeum blackish; gaster with distal part of tergite 5 and tergites 6+ infusate. Pterostigma and *Rs+2r* blackish, other veins flavous; wing hyaline, proximal angle of marginal cell infumate.

REMARKS. This species has been taken at light in cloud forests between 1500 and 2350 m in Costa Rica. Nothing is known of its biology.

MATERIAL EXAMINED

Holotype ♂, **Costa Rica**: Alajuela Prov; Volcan Poas N. P., xii.1982 (*Janzen & Hallwachs*) (BMNH).

Paratypes. **Costa Rica**: 1 ♂, same data as holotype (BMNH); 1 ♂, same locality as holotype, xii.1981 (*Janzen & Hallwachs*) (BMNH); 1 ♀, Monte Verde Reserve, 1500 m, ii.1980 (*Mason*) (TC).

RIEKOPHION Gauld

Riekophion Gauld, 1977: 21. Type-species: *Allocomptus emandibulator* Morley, by original designation.

Mandibles not twisted, weakly evenly tapered or distally parallel-sided, subequally bidentate; outer mandibular surface flat, punctate. Maxillary palp 5-segmented, labial palp 4-segmented; clypeus in profile convex, margin usually blunt, in one species, impressed; clypeus in anterior aspect from weakly convex to slightly concave. Ocelli from large, the hind ones contiguous with eyes, to rather small, the hind ones separated from eyes by 0.5 times their minimum diameter; frontal carina absent, or weakly present in one species; occipital carina usually complete, in one species ventrally obsolescent, not reaching hypostomal carina. Antennae moderately long and relatively slender, at least 1.3 times length of fore wing. Pronotum either unspecialized, or in two species mediodorsally long and flat; spiracular sclerite exposed, or in one species with slight expansion of dorsal lobe of pronotum; notauli vestigial or absent; epicnemial carina complete, generally curved to meet anterior margin of pleuron; mesopleural furrow very weak to quite distinct diagonally. Scutellum weakly convex, very characteristic in being fairly narrow and barely tapered, and medially longitudinally higher than laterally; carinae if present only on anterior 0.3 or less; posterior transverse carina of mesosternum complete. Propodeum with anterior area moderately to very long, often irregularly striate; propodeum usually with anterior and posterior transverse carinae complete, latero-median ones weaker but often complete behind anterior transverse carina and usually enclosing a long narrow area superomedia. Fore wing with pterostigma moderately to very slender; marginal cell usually long; *Rs+2r* proximally sinuous, only weakly broadened and not curved abruptly to join the pterostigma, unusual in joining stigma distal to proximal end; discosubmarginal cell anteriorly glabrous, often with group of isolated hairs near base of *Rs+2r*, always bearing a detached corneous or sclerotized patch in membrane. *1m-cu* weakly sinuous or fairly evenly curved. Hind wing with *Rs* straight or very weakly curved. Fore tibial spur with a membranous flange behind macrotrichial comb; mid and hind trochantelli unspecialized; inner hind tibial spur flattened, the margin with close long hairs; hind tarsal claws elongate, with thyridia small, widely separated from anterior margin to which it is joined by a groove; umbo absent; epipleuron up-turned. Ovipositor sheath slender; unusual in having male subgenital plate ornamented with projections.

Riekophion is a very distinctive genus, characterized by the quadrate scutellum, unusual venation and

ornamented subgenital plate (Gauld, 1977). It contains three species which occur in southern and western Australia. The phylogenetic inter-relationships of these species are suggested in Fig. 28. Nothing is known of the biology of these insects.

SICOPHION Gauld

Sicophion Gauld, 1979: 71. Type-species: *Sicophion pleuralis* Gauld, by original designation.

Mandibles stout, twisted about 25–35° and with lower tooth slightly the longer; outer mandibular surface more or less flat, sparsely punctate. Maxillary palp 5-segmented, labial palp 4-segmented; maxillae elongate; clypeus in profile convex, apical margin not impressed, in anterior aspect truncate. Ocelli very large, the posterior ones close to margin of eye; frontal carina absent; occipital carina mediodorsally incomplete, ventrally obsolescent, not reaching hypostomal carina. Antennae very long and slender, at least 1.4 times length of fore wing. Pronotum unspecialized; spiracular sclerite virtually completely occluded by enlarged flap formed from hind corner of pronotum; notauli absent; epicnemial carina strong, extending onto mesopleural furrow; mesopleural furrow strong, extending from episternal scrobe forward. Scutellum quite convex, narrow, carinate only on anterior 0.2–0.3; posterior transverse carina of mesosternum present only laterally as vestiges. Propodeum with anterior area occluded; anterior transverse carina present centrally, laterally obsolescent; posterior transverse carina present as lateral vestiges; propodeum otherwise rather smooth, posterior area not differently sculptured from spiracular area. Fore wing with pterostigma broad, distally abruptly narrowed; marginal cell moderately long and slender, unique amongst ophonines in being broadest distad of centre at situation in distal abscissa of *Rs*; *Rs+2r* not angled near junction with pterostigma, but somewhat broadened, somewhat angled slightly proximal to centre; discosubmarginal cell very extensively glabrous anteriorly, the glabrous area bearing indistinct corneous areas; *1m-cu* without a ramellus, rather abruptly curved. Hind wing with *Rs* unique in the Ophoninae in being slightly convex. Fore tibial spur with membranous flange behind macrotrichial comb; mid and hind trochantelli very elongate, but unspecialized; inner hind tibial spur strongly flattened with a fringe of long, close hairs; hind tarsal claws unspecialized, markedly sexually dimorphic, those of male being far more closely pectinate than those of the female. Gaster exceptionally slender; tergite 2 elongate, thyridia absent; umbo absent; epipleuron very narrow, pendant. Ovipositor sheath slender, ovipositor unique in being proximally angled and without a subapical notch.

Sicophion is a small Neotropical genus with a single described Bolivian species (Gauld, 1979). In the BMNH is a short series of a putative second species collected in Costa Rica by Janzen & Hallwachs. These differ from *S. pleuralis* in having a more extensive glabrous area in the discosubmarginal cell and a less obviously 'bent' *Rs+2r*. There are subtle differences in colour and head shape also.

Sicophion is one of the most distinctive of ophonine genera. The sinuous *Rs* in the fore wing, the slightly convex *Rs* in the hind wing and the basally angulate, acutely pointed ovipositor with no subapical notch are, amongst ophonines, unique autapomorphies of the genus. Their very slender form with extensive semi-matt black coloration is a typical feature of ophonines from higher elevations (e.g. *Enicospilus ruwenzorius* Gauld & Mitchell) and the rather elongate head shape is also found in some upper montane species (e.g. *Ophion longiceps* (Townes), Gauld & Mitchell, 1981). The presumed loss of the dorsal notch is a feature that occurs in several genera of ichneumonids with more slender ovipositors (e.g. *Parania* in the Anomaloninae, Gauld, 1976).

Sicophion species are only known to occur at mid and high elevation in the Neotropical region. Specimens have been taken between 1600 and 3000 m. Nothing is known of their host ranges.

The *EREMOTYLUS* genus-group

This group contains three genera, *Eremotylus*, *Trophophion* and *Hellwigiella*. The last two are monobasic and probably really represent single phenetically highly divergent species of *Eremotylus*. The majority of species of all genera are eremic organisms.

The *Eremotylus* genus-group is characterized by the fore wing venation; *Rs+2r* is strongly geniculate and thickened before joining the pterostigma whilst *1m-cu* is usually fairly evenly arcuate. The clypeus is usually flat or out-flared and the margin is not subapically impressed.

EREMOTYLUS Foerster

Eremotylus Foerster, 1869: 150. Type-species: *Ophion marginatus* Gravenhorst (= *Anomalon marginatum* Jurine), by subsequent monotypy, Thomson, 1888: 1193.

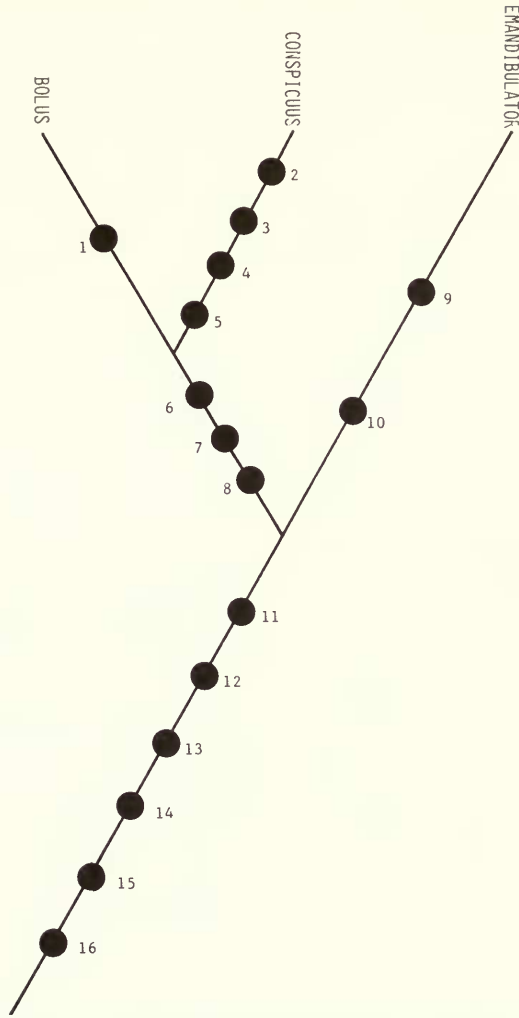


Fig. 28 Suggested phylogenetic inter-relationships of species of *Riekophion*. The apomorphic characters supporting this arrangement are: 1, mandible slender; 2, ocelli small; 3, occipital carina mediodorsally broadened; 4, body extensively black; 5, pronotal lobe expanded; 6, pronotum medio-dorsally flat and lengthened; 7, presence of hair patch in fenestra; 8, cubital index small; 9, distal sclerite lost; 10, ocelli grossly enlarged; 11, scutellum quadrate; 12, possession of alar sclerites; 13, metapleuron inflated; 14, R_s+2r sinuous; 15, R_s+2r joining pterostigma near centre; 16, male subgenital plate ornamented.

Camptoneura Kriechbaumer, 1901: 23. Type-species: *Ophion marginatus* Gravenhorst (= *Anomalon marginatum* Jurine), by subsequent designation, Viereck, 1914: 27. [Junior homonym of *Camptoneura* Agassiz, 1846.]

Genophion Felt, 1904: 123. Type-species: *Genophion gilletti* Felt (= *Ophion costale* Cresson), by original designation.

Camptoneuroides Strand, 1928: 52. [Replacement name for *Camptoneura* Kriechbaumer.]

Clistorapha Cushman, 1947: 450. Type-species: *Ophion subfuliginosus* Ashmead, by original designation.

Boethoneura Cushman, 1947: 450. Type-species: *Boethoneura arida* Cushman, by original designation.

Chilophion Cushman, 1947: 450. Type-species: *Ophion abnormum* Felt, by original designation.

Chlorophion Townes, 1971: 55. Type-species: *Chlorophion vitripennis* Townes, by original designation.

Mandibles not twisted, usually quite long, moderately strongly narrowed, usually subequally bidentate or with upper tooth slightly the longer; outer mandibular surface flat or slightly convex, punctate. Maxillary palp 5-segmented, labial palp 4-segmented; clypeus in profile more or less flat or even slightly out-flared, margin never impressed; clypeus in anterior aspect truncate or slightly concave. Ocelli usually moderately large to large, the posterior ones separated from the eyes by less than 0.5 their own maximum diameter, or in a few species with the ocelli small and the posterior ones separated from the eyes by more than their own maximum diameter; frontal carina absent or rarely very faintly indicated; occipital carina complete, rarely ventrally somewhat obsolescent. Antennae moderately long, at least 1.2 times length of the fore wing. Pronotum unspecialized; spiracular sclerite exposed; notauli vestigial or absent; epicnemial carina usually complete; mesopleural furrow usually rather weak but discernible, faintly indicated between episternal scrobe and subalar prominence. Scutellum weakly convex, usually carinate 0.3 to 0.8 of its length, rarely without carinae; posterior transverse carina of mesosternum from complete to present only laterally as vestiges. Propodeum generally with anterior area short but not occluded, in some species moderately long; anterior transverse carina usually distinct, at least centrally, sometimes complete, rarely absent; posterior transverse carina present laterally as vestiges or absent, other carinae generally absent; posterior area from smooth and polished to rugulose. Fore wing with pterostigma moderately slender; marginal cell long and slender, rarely rather short; R_s+2r abruptly geniculate and thickened near pterostigma; discosubmarginal cell with a small glabrous area in anterior corner; $1m-cu$ without a ramellus, arcuate or very weakly sinuous. Hind wing with R_s from almost straight to strongly curved. Fore tibial spur with a membranous flange behind macrotrichial comb; mid and hind trochantelli unspecialized; inner hind tibial spur generally flattened with a marginal fringe of close hairs; hind tarsal claws usually unspecialized, sometimes slightly longer and less evenly curved than normal. Gaster slender; tergite 2 in profile elongate with thyridia separated from fore margin by its own length or a little more, characteristically at the posterior end of a weak trough; umbo usually distinct, rarely weak; epipleuron up-turned. Ovipositor sheath slender.

Eremotylus is a moderately large genus containing about 35 species, most of which occur in the drier regions around the Mediterranean, the Middle East, Central Asia, the south-western United States and northern Mexico. Isolated species have a wider distribution; *E. subfuliginosus* occurs in the north-eastern part of the U.S.A., whilst the morphologically very specialized species *E. marginatus* is not uncommon throughout much of western Europe. *E. vitripennis* occurs in the drier parts of southern South America, whilst *E. perdis* occurs in the Indian subcontinent (Gauld & Mitchell, 1981). The Palaearctic species were monographed recently by Horstmann (1981) who recognized eight species. The New World species are extremely poorly known. Virtually nothing is known about the host ranges of species of *Eremotylus*. The only reliable host record to hand is of one European species (*E. curvinervis* Kriechbaumer) which has been reared from a species of *Dryobota* Lederer (Lepidoptera: Noctuidae) (Seyrig, 1926).

Some authors (e.g. Cushman, 1947; Townes, 1971) divided the species of *Eremotylus* between a number of small genera characterized mostly by differences in the development of carinae, particularly the transverse mesosternal carina. Gauld (1979) pointed out that despite these differences, all species share a large number of features and seem to comprise a natural group. Horstmann (1981) accepted this treatment. The present study has reinforced the author's opinion that this is a natural group; it is definable on the basis of several apomorphies including the characteristically modified R_s+2r , the arcuate or slightly sinuous $1m-cu$ and the unoccluded anterior propodeal area. The characteristic clypeus and rather slender, longish mandibles are useful confirmatory characters.

The present disjunct distribution of the genus suggests that at one time the range of the genus must have been wider. Further discussion of zoogeography is best left until the New World species are better known.

HELLWIGIELLA Szépligeti

Hellwigiella Szépligeti, 1905: 23. Type-species: *Hellwigiella nigripennis* Szépligeti, by subsequent designation, Viereck, 1914: 67.

Mandible twisted about 15°, not appreciably narrowed, with upper tooth slightly shorter than the lower and bearing a pronounced very sharp ventral flange; outer mandibular surface punctate, with a strong proximal concavity. Maxillary palp 5-segmented, labial palp 4-segmented; clypeus in profile quite convex centrally, with margin reflexed, quite thin; clypeus in anterior aspect almost truncate. Ocelli small, the posterior ones separated from eye margin by more than their own maximum diameter; frontal carina absent; occipital carina strong, ventrally joining hypostomal carina. Antennae short and stout, central segments transverse, the flagellum barely longer than the fore wing. Pronotum mediodorsally quite long, otherwise unspecialized; spiracular sclerite exposed; notauli absent; epicnemial carina strong, complete; mesopleural furrow vestigial. Scutellum quite convex, laterally carinate about 0.8 of its length; posterior transverse carina of mesosternum complete or obsolescent centrally. Propodeum with anterior area quite short, impressed as a

deep U-shaped groove; anterior transverse carina more or less complete, other carinae indistinct, posterior area reticulate. Fore wing with pterostigma moderately stout; marginal cell quite long and slender; *Rs+2r* abruptly geniculate and slightly broadened before joining pterostigma; discosubmarginal cell with a very small glabrous area anteriorly; *1m-cu* evenly curved, usually without a ramellus. Hind wing with *Rs* evenly bowed. Fore tibial spur with a membranous flange behind macrotrichial comb; mid and hind trochantelli unspecialized; inner hind tibial spur almost cylindrical, with a fringe of sparse hairs; hind tarsal claw quite long and weakly curved. Gaster moderately slender, tergite 2 about twice as long as deep with thyridia separated from anterior margin by about their own length; umbo distinct; epipleuron membranous, pendant in most individuals. Ovipositor sheath slender.

Hellwigiella contains what is, I believe, a single Mediterranean species, though it is sculpturally and chromatically rather variable and has been divided into two (Szépligeti, 1905). *Hellwigiella* is morphologically extremely distinctive on account of the characteristic clypeus and mandible, and the form of the propodeum. The majority of apomorphic features characterizing the genus are obviously adaptations to a diurnal existence and most are paralleled in other genera with similar habits. It is possible that *Hellwigiella* is merely a specialized diurnal offshoot of *Eremotylus*, but if this were so then it is necessary to postulate that the specialized invaginated condition of the anterior area of the propodeum (character 22·2) has been derived from the partially elongated condition of *Eremotylus* (character 22·1). In the preceding phylogenetic analysis it has been suggested that the apomorphic states of these characters represent alternative specializations, so it is possible that *Eremotylus* and *Hellwigiella* have a sister-group relationship. Nothing is known of the biology of *Hellwigiella*.

TROPHOPHION Cushman

Trophophion Cushman, 1947: 447. Type-species: *Trophophion tenuiceps* Cushman, by original designation.

Mandibles barely twisted, quite stout, weakly narrowed, subequally bidentate; outer mandibular surface weakly convex. Maxillary palp 5-segmented, labial palp 4-segmented; maxilla and labium elongate, projecting below mandibles; clypeus in profile flat, in anterior aspect almost truncate. Ocelli small, the posterior ones separated from the eye by more than their own maximum diameter; frontal carina absent; occipital carina complete dorsally, ventrally incomplete. Antennae short, slightly clavate, barely longer than fore wing. Pronotum unspecialized; spiracular sclerite exposed; notauli absent; epicnemial carina complete; mesopleural furrow indistinct. Scutellum weakly convex, without lateral carinae; posterior transverse carina of mesosternum present only laterally as vestiges. Propodeum with anterior area short but not occluded; anterior transverse carina present medially, posterior one present laterally as vestiges, other carinae obsolescent; posterior area polished, punctate. Fore wing with pterostigma moderately slender; marginal cell moderately short; *Rs+2r* thickened and curved to join pterostigma; discosubmarginal cell with glabrous area anteriorly; *1m-cu* evenly curved, without a ramellus. Hind wing with *Rs* bowed. Fore tibial spur with a membranous flange behind macrotrichial comb; mid and hind trochantelli unspecialized; inner hind tibial spur weakly flattened, fringed with long fine hairs; tarsal claws rather long and weakly curved. Gaster moderately stout and rather more cylindrical than that of most ophionines; tergite 2 in profile less than twice as long as posteriorly deep, with thyridia separated from anterior margin by about its own length; umbo rather weak; epipleuron up-turned. Female with tergites 3–7 shallowly notched medially, with subgenital plate large, strongly sclerotized and centrally notched; ovipositor and sheath rather stout.

Only a single species of *Trophophion* is known. This occurs in the drier south-west of the U.S.A. Its host is unknown. *Trophophion* is recognizable on account of the specializations of the head and mouthparts and the female gaster. In other respects it is very similar to some *Eremotylus* species, and it is almost certainly a specialized offshoot of this genus. However, I have hesitated to synonymize *Trophophion* until some details of its biology and host relationship are known. If these are very different from those of *Eremotylus* then I suggest it be left as a separate genus even though this leaves *Eremotylus* as a paraphyletic taxon. Additional material from the dry parts of the U.S.A. and northern Mexico might help in elucidating the phylogenetic position of this bizarre species.

The THYREODON genus-group

This group contains five genera, *Barytatocephalus*, *Euryophion*, *Thyreodon*, *Rhynchophion* and *Dictyonotus*. The first of these is included in the complex on the basis of three apomorphies, the possession of an impressed anterior propodeal area (22·2), long, weakly curved tarsal claws, and

absence of any transverse carinae on the propodeum. *Barytatocephalus* lacks the tilted mandibular axis, slender pterostigma and cylindrical hind tibial spurs of other genera, and thus seems to constitute the most primitive branch of the lineage. The remaining genera form a holophyletic group, and this may be divided into two holophyletic subgroups, one comprising *Thyreodon*, *Dictyonotus* and *Rhynchophion*, the other containing just *Euryophion*. The former subgroup is defined by the possession of a pointed clypeus, a very short and stout flagellum and an exceptionally elongate propodeal spiracle. A further possible apomorphy of this lineage is the possession of an evenly hirsute anterior part of the discosubmarginal cell (assuming that presence of a small glabrous area is an apomorphy of the subfamily). *Euryophion* has a slightly concave clypeus and a somewhat thickened and usually proximally curved *Rs+2r*. These two lineages seem to be biologically distinct; species of the *Thyreodon* subgroup have only been recorded as parasites of Sphingidae (Gauld & Mitchell, 1978; 1981; Carlson, 1979), whilst *Euryophion* species attack Eupterotidae and Saturniidae.

The close relationship between *Dictyonotus*, an Old World genus, and *Rhynchophion* and *Thyreodon*, primarily Neotropical genera, suggests they may have had a common ancestor that was widely distributed throughout the Nearctic and eastern Palaearctic regions. *D. purpurascens*, which could well be rather similar to the group ancestor, is currently widely distributed in the eastern Palaearctic, occurring as far north as 50° (Townes *et al.*, 1965), so a slight extension of its range northwards would have permitted migration across the Bering Strait. Movement from Asia to America is postulated on the belief the group has had an Old World origin, a suggestion favoured by the present distribution of the most primitive member of the group (*Barytatocephalus*) and the sister-lineage of the *Thyreodon* subgroup (*Euryophion*).

The exact relationship between the genera *Thyreodon*, *Rhynchophion* and *Dictyonotus* is unclear, as slight evidence in the form of a very few highly homoplastic characters can be marshalled for placing *Thyreodon* as the sister-group of either *Rhynchophion* or *Dictyonotus*, or

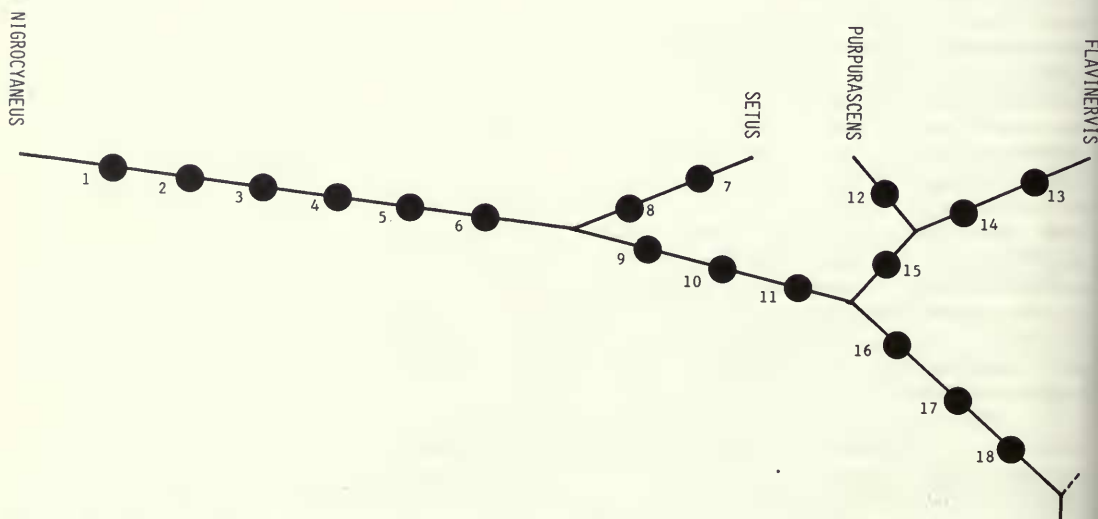


Fig. 29 Suggested phylogenetic inter-relationships of *Dictyonotus* species. The length of the lines is proportional to the number of apomorphies characterizing it. The apomorphic characters supporting this arrangement are: 1, presence of a metapleural tubercle; 2, striation present on gena; 3, hind tarsus flattened; 4, *1m-cu* sinuous; 5, body densely pubescent; 6, tergite 2 posteriorly deeper than long; 7, malar space longer than basal mandibular width; 8, occipital carina mediodorsally broadened; 9, petiole depressed; 10, tergite 2 posteriorly at least as deep as long; 11, petiolar spiracles anterior to margin of sternite; 12, presence of metanotal swelling; 13, reduction in number of hamuli; 14, development of strongly punctate scutellum; 15, thyridia remote from anterior margin of tergite; 16, complete posterior transverse carina of mesosternum (? a reversal); 17, presence of tubercle on metanotal margin; 18, epipleuron 2 pendant.

even *Rhynchophion* + *Dictyonotus* (see p. 93). What is clear is that both *Rhynchophion* and, more particularly, *Thyreodon*, are characterized by a string of apomorphies (as is *nigrocyaneus*), whilst *purpurascens* may well have changed very little from the form of the group ancestor (Fig. 29). One wonders what adaptation acquired by the *Thyreodon* lineage has allowed it to radiate so markedly in the Neotropics and give rise to a complex of 30 or more quite closely related species attacking sphingids, whilst in Asia, *Dictyonotus*, although presented with a very similar diversity of potential hosts (Rothschild & Jordan, 1903), has apparently failed to radiate appreciably.

BARYTATOCEPHALUS Schulz

Barycephalus Brauns, 1895: 43. Type-species: *Barycephalus mocsaryi* Brauns, by subsequent designation, Viereck, 1914: 19. [Homonym of *Barycephalus* Guenther, 1860.]
Barytatocephalus Schulz, 1911: 23. [Replacement name for *Barycephalus* Brauns.]

Mandible not twisted, very weakly narrowed, with upper tooth a little stouter but no longer than the lower; outer mandibular surface with a strong proximal concavity, and with a weak trace of a diagonal groove. Maxillary palp 5-segmented, labial palp 4-segmented; clypeus in profile convex, margin impressed, acute; clypeus in anterior aspect weakly convex. Ocelli small, the posterior ones remote from the eyes; frontal carina absent, though a small trace may be discernible in some specimens; occipital carina complete, ventrally reaching to hypostomal carina. Antennae quite short, about 1.3 times as long as fore wing, central segments slightly elongate. Pronotum unspecialized; spiracular sclerite exposed; notauli absent; epicnemial carina complete, present on mesopleuron; mesopleural furrow weak but discernible as a short diagonal impression extending from episternal scrobe towards subalar prominence. Scutellum convex, carinate laterally only on anterior 0.4; posterior transverse carina of mesosternum complete. Propodeum convex, with anterior area impressed as a deep groove; propodeal carinae absent; posterior area coarsely punctate. Fore wing with pterostigma moderately slender; marginal cell moderately long; $R_s + 2r$ slender, proximally almost straight; discosubmarginal cell with a small glabrous area at anterior corner, remainder of cell sparsely hirsute; $1m-cu$ somewhat irregularly convex, without a ramellus. Hind wing with R_s virtually straight; genus unusual in having distal abscissa of Cu_1 very weak and the first abscissa of Cu_1 and $cu-a$ forming an almost straight line, oblique, so anterior corner of first submarginal cell is about 50° . Fore tibial spur without membranous flange behind macrotrichial comb; mid and hind trochantelli simple; inner hind tibial spur somewhat flattened (though less so than in most taxa in this subfamily), with a fringe of moderately long hairs; hind tarsal claws long, weakly curved. Gaster moderately slender; tergite 2 in profile with thyridia close to anterior margin, elongate, umbo vestigial; epipleuron up-turned. Ovipositor slender.

Barytatocephalus is a small genus containing a single species that is widely distributed throughout the eastern Mediterranean region and the southern U.S.S.R. Nothing is known of its biology.

DICTYONOTUS Kriechbaumer

Dictyonotus Kriechbaumer, 1894a: 198. Type-species: *Dictyonotus melanarius* Kriechbaumer (= *Thyreodon purpurascens* Smith), by monotypy.
Aglaophion Cameron, 1903: 131. Type-species: *Aglaophion flavinervis* Cameron, by monotypy.
Ophionopsis Tosquinet, 1903: 389. Type-species: *Ophionopsis fulvipes* Tosquinet (= *Ophionopsis nigrocyaneus* Tosquinet), by subsequent designation, Viereck, 1914: 106. **Syn. n.**
Hybopleurax Enderlein, 1912: 624. Type-species: *Hybopleurax sumatranum* Enderlein (= *Thyreodon purpurascens* Smith), by monotypy.
Hypselogastrina Enderlein, 1918: 217. Type-species: *Hypselogastrina saliina* Enderlein (= *Ophionopsis nigrocyaneus* Tosquinet), by original designation. **Syn. n.**
Coracophion Shestakov, 1926: 260. Type-species: *Coracophion manganicolor* Shestakov (= *Thyreodon purpurascens* Smith), by monotypy.

Mandibles stout, not twisted, barely narrowed distally, equally bidentate or with lower tooth slightly the longer; outer mandibular surface more or less flat, with scattered hairs. Maxillary palp 5-segmented, labial palp 4-segmented; clypeus in profile flat, with margin often slightly out-flared, in anterior aspect convex with a median obtuse point. Ocelli small, the hind ones separated from the eye margins by at least their own minimum diameter; frontal carina present; occipital carina complete, ventrally usually not joining the hypostomal carina. Pronotum unspecialized; spiracular sclerite exposed; notauli absent; epicnemial carina more or less complete, always present on mesopleuron; mesopleural furrow weakly impressed, horizontal,

extending from episternal scrobe to near upper end of epicnemial carina. Scutellum moderately convex, with longitudinal lateral carinae present only on anterior end; posterior transverse carina of mesosternum complete; metanotum exceptional in being produced into a blunt prominence above upper end of spiracle. Propodeum with anterior area short, impressed as a deep groove; propodeal carinae absent or with vestiges of lateromedian ones discernible; posterior area convex, rugose-reticulate. Fore wing with pterostigma slender; marginal cell of moderate length; $Rs+2r$ very slightly bowed proximally, not appreciably broadened; $1m-cu$ evenly curved to somewhat sinuous, without a ramellus; discosubmarginal cell evenly hirsute anteriorly. Hind wing with Rs weakly curved or almost straight. Fore tibial spur without a membranous flange behind macrotrichial comb; mid and hind trochantelli unspecialized; inner hind tibial spur cylindrical, without a row of long marginal hairs; hind tarsal claws long and weakly curved. Gaster stout to very stout; tergite 2 in profile from about 1.5 times as long as posteriorly deep to less than 1.0 times as long as deep, with thyridia oval, separated from anterior margin by about its own diameter or more; umbo absent; epipleuron pendant. Ovipositor sheath slender.

This genus contains four species, *D. purpurascens* (Smith), *D. flavinervis* (Cameron) from the Oriental and eastern Palaearctic regions and *D. nigrocyaneus* (Tosquinet) **comb. n.** and *D. setus* (Gauld & Mitchell) **comb. n.** from the Afrotropical region. The last two were formerly placed in *Ophionopsis*, a genus originally proposed to accommodate the morphologically aberrant *nigrocyaneus*. *D. setus* is much more similar to the main *Dictyonotus* line than is *nigrocyaneus*, suggesting the two genera should be united (Gauld & Mitchell, 1978). The *Dictyonotus* lineage is distinguished only by one weak apomorphy (Fig. 29), and *purpurascens* in turn by a further one, suggesting this species may resemble the ancestor of this genus, and also the ancestors of *Rhynchophion* and *Thyreodon*.

The hosts of *Dictyonotus* are apparently the larvae of Sphingidae (Townes *et al.*, 1965; Gauld & Mitchell, 1978; 1981).

EURYOPHION Cameron

Euryophion Cameron, 1906: 83. Type-species: *Euryophion nigripennis* Cameron, by monotypy.

Eurycamptus Morley, 1912: 27. Type-species: *Ophion latipenne* Kirby, by subsequent designation, Viereck, 1914: 57.

Thoracophion Roman, 1943: 22. Type-species: *Thoracophion ventrator* Roman (= *Ophion latipenne* Kirby), by monotypy.

Primophion Townes, 1971: 65. Type-species: *Primophion adustus* Townes, by original designation.

Rictophion Townes, 1971: 66. Type-species: *Euryophion nebulifer* Morley (= *Cymatoneura ikuthana* Kriechbaumer), by original designation. **Syn. n.**

Mandibles large, not twisted, weakly narrowed apically, subequally bidentate. Maxillary palp 3–5 segmented, labial palp 3–4 segmented; clypeus in profile flat or with apex out-turned, in anterior aspect usually with margin slightly concave. Ocelli small to large; frontal carina present or absent; occipital carina usually complete, rarely dorsally incomplete. Antennae rather stout, not longer than fore wing. Pronotum unspecialized, spiracular sclerite exposed; notauli weak or vestigial; epicnemial carina present ventrally, sometimes laterally absent; mesopleural furrow usually vestigial. Scutellum without lateral carinae; hind margin of metanotum at the most only weakly swollen before propodeal spiracle; posterior transverse carina of mesosternum absent except for lateral and rarely central vestiges. Propodeum with anterior area short, impressed as a deep trough; carinae virtually absent though their former position may be indicated by rugosities; posterior area from punctate to finely wrinkled to coriaceous. Fore wing with pterostigma slender; marginal cell moderately long; $Rs+2r$ abruptly curved and thickened basally; discosubmarginal cell without a distinct fenestra, but usually with a small glabrous area in anterior corner; $1m-cu$ fairly evenly curved, without a distinct ramellus. Hind wing with Rs from weakly to strongly curved. Fore tibial spur without a membranous flange behind macrotrichial comb; mid and hind trochantelli simple; inner hind tibial spur subcylindrical or slightly flattened, often with a reduced fringe of hairs; hind tarsal claws long and weakly curved, rarely with a small apical flange. Gaster stout, tergite 2 in profile short and deep, generally less than 3 times as long as deep posteriorly; thyridia present or absent; umbo vestigial; epipleuron pendant or up-turned. Ovipositor sheath slender, often concealed.

Although no character is a unique autapomorphy of this genus, the species share a large number of apomorphic features (p. 87). They resemble each other greatly in venation, shape of the gaster and form of the head. No other ophionines have reduced palpal segments nor do any have the claw flange found in some more specialized *Euryophion*. The initial analysis suggested that *Euryophion* is paraphyletic with respect to *Rictophion*. In order to resolve this matter further a more detailed analysis was undertaken using all species in the two genera, and this confirmed the paraphyletic nature of *Euryophion*. The sole

representative of *Rictophion*, *R. ikuthana*, can be considered a specialized species of *Euryophion*, and it is on this basis that *Rictophion* is here treated as a synonym.

The more detailed analysis involved eight species, *E. latipennis* (201), *E. adustus* (202), *E. ikuthana* (203), *E. nigripennis* (204), *E. meridionalis* (205), *E. variegatus* (206), *E. vexatious* (207) and *E. pisinnus* (208). Eighteen characters from the original set (1.1, 8.1, 8.2, 9, 13, 18.2, 19, 27.2, 29.1, 29.2, 30, 36.1, 36.2, 37, 43.2, 54, 57 and 59) were used together with the following eight characters.

- 70 Labrum shape. In most ichneumonids the labrum is either semicircular or triangular, but broader basally than medially long; some *Euryophion* are specialized in having the labrum longer than broad (1).
- 71 Hind tarsal claw. In some *Euryophion* the hind claw is specialized in having a small flange near the apex (1).
- 72 *Rs* in hind wing. The moderately curved condition is considered plesiomorphic for *Euryophion*; in some taxa it is strongly curved (1).
- 73 Wing patterning. The plesiomorphic condition for ophionines (and members of out-groups) is unpatterned wings. In some *Euryophion* species the fore wings are distinctly patterned (1).
- 74 Wing ground colour. Transparent, virtually colourless wings are plesiomorphic for ophionines. The strongly infumate condition found in some *Euryophion* species is considered to be a derived feature (1).
- 75 *Rs* in fore wing. The plesiomorphic condition is for this vein to be simply arcuate. The sinuous condition of a few species of *Euryophion* is considered to be derived (1).
- 76 Rugosity of propodeum. The plesiomorphic condition for *Euryophion* species and related genera appears to be possession of at least some rugae close to the position of the vestigial carinae; the smooth, punctate propodeum of one *Euryophion* species is considered to be derived (1).
- 77 Hairiness of ovipositor sheath. The plesiomorphic condition for most ophionines, and other ichneumonids, is for the sheath to bear close, moderately long pubescence. The short sparse pubescence of one species is considered to be a derived characteristic (1).

The primary data matrix obtained (Table 20) was analysed using the methods outlined in the generic analysis. Characters 8.1, 18.2, 29.1, 29.2, 76 and 77 each have only a single derived state and therefore make no contribution to resolving phylogenetic relationships. A LeQuesne test on the remaining data set (Table 21) showed three characters (9, 59, 74) to be particularly homoplastic. Removal of these caused an improvement in the overall O/E ratio from 0.62 to 0.45. The high values evident in the labels matrix

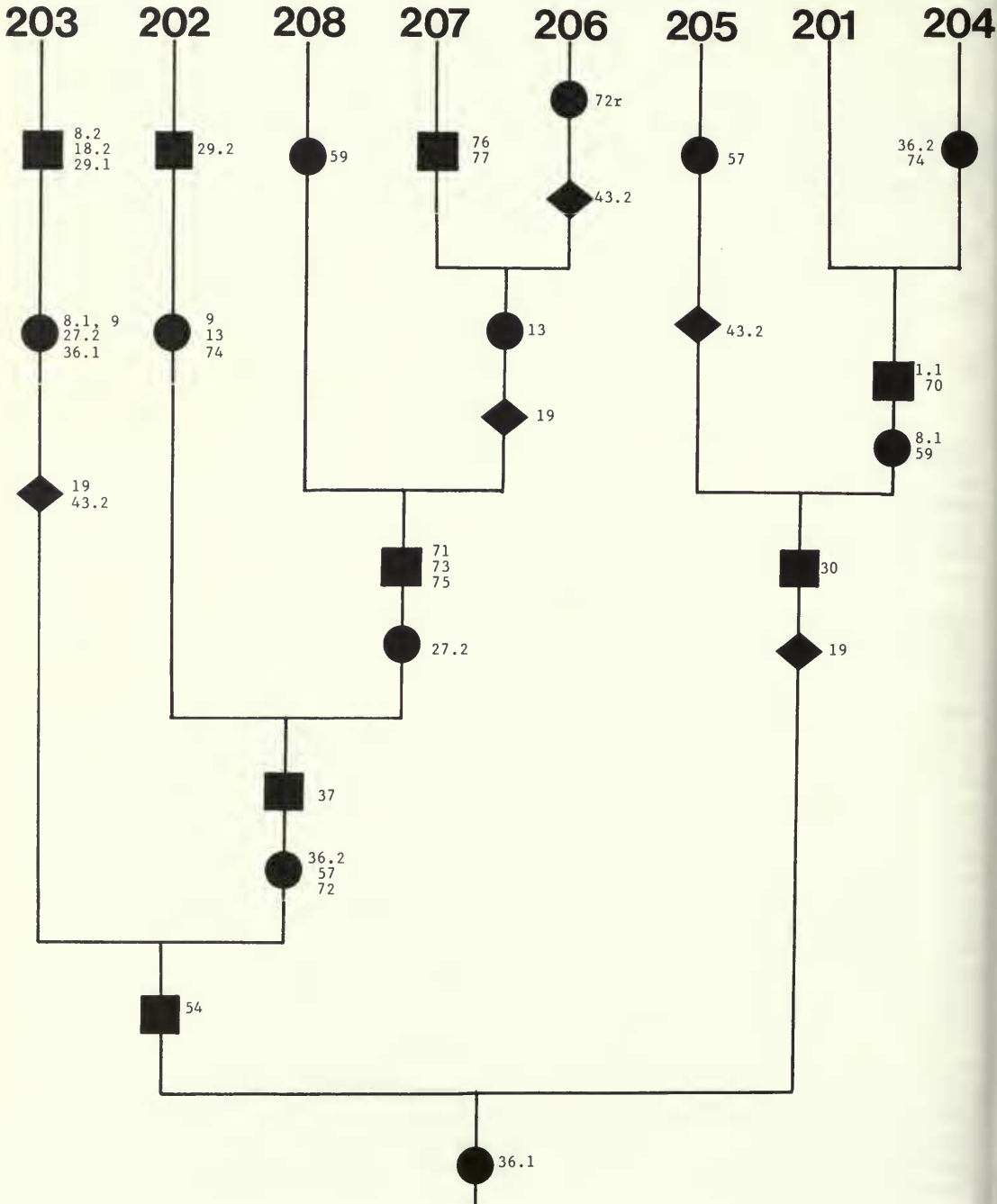
Table 20 Primary data matrix for genus *Euryophion*. The taxa corresponding to the numbers are given in the text (p. 137).

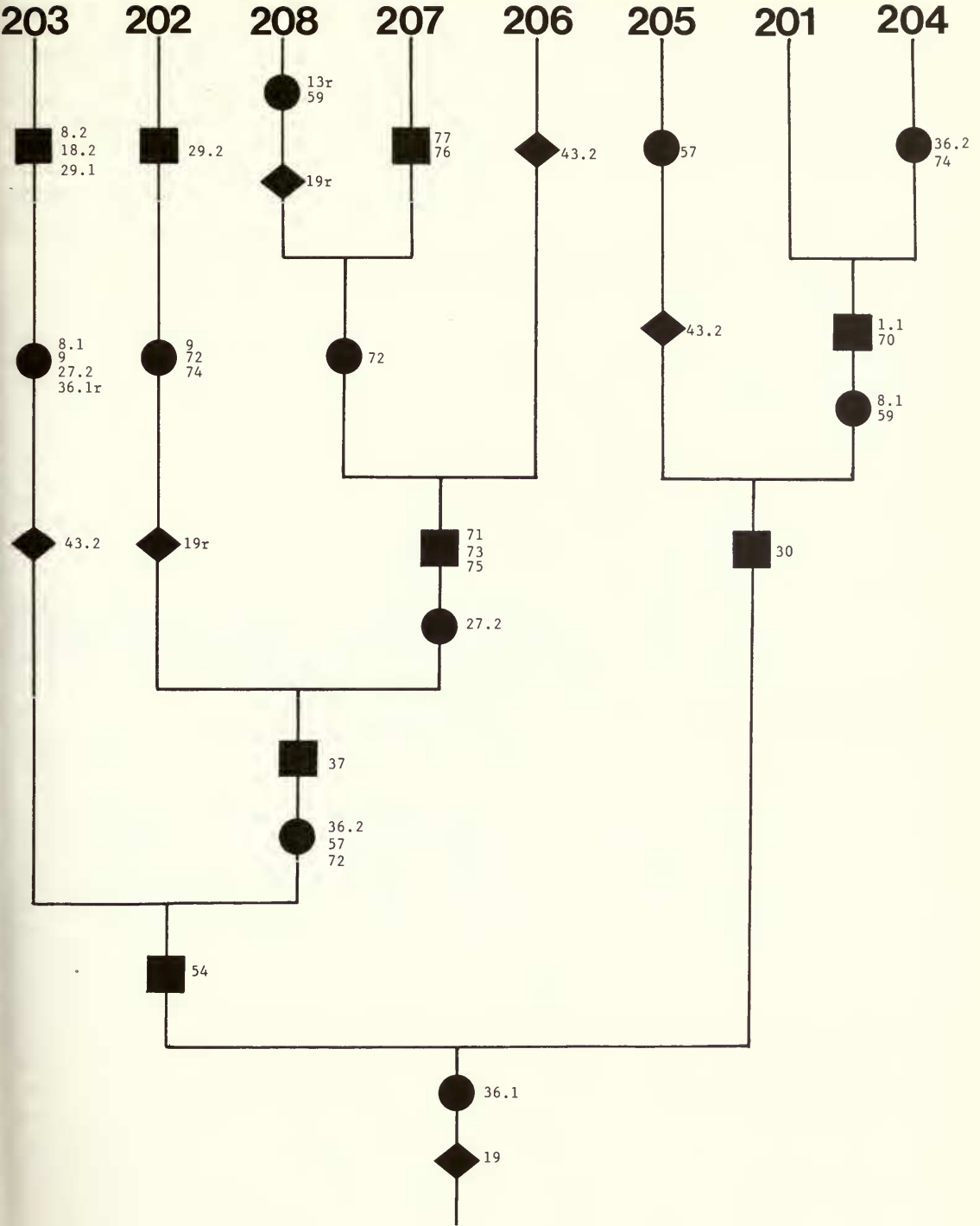
| | 1.1 | 8.2 | 13 | 19 | 29.1 | 30 | 36.2 | 43.2 | 57 | 70 | 72 | 74 | 76 | 77 |
|-----|-----|-----|------|------|------|------|------|------|----|----|----|----|----|----|
| | 8.1 | 9 | 18.2 | 27.2 | 29.2 | 36.1 | 37 | 54 | 59 | 71 | 73 | 75 | | |
| 201 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 |
| 202 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 |
| 203 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 204 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 |
| 205 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 |
| 206 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 |
| 207 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 |
| 208 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 0 |

Table 21 Results of LeQuesne test on *Euryophion* data matrix. Conventions as in Table 2.

| Character number: | Failures observed | expected | O/E ratio |
|-------------------|-------------------|----------|---|
| <u>1.1</u> : 2 | 9.3 | 0.22 | <u>8.1</u> : 8 13.2 0.60 |
| <u>19</u> : 8 | 9.3 | 0.86 | <u>30</u> : 6 13.2 0.45 |
| <u>37</u> : 5 | 14.1 | 0.35 | <u>54</u> : 6 13.2 0.45 |
| <u>59</u> : 13 | 13.2 | 0.98 | <u>71</u> : 5 13.2 0.38 |
| <u>73</u> : 5 | 13.2 | 0.38 | <u>75</u> : 5 13.2 0.38 |
| Grand totals- | failures observed | expected | O/E ratio |
| | 72 | 116.7 | 0.62 |
| Ranking ratios | | | |
| 1.1 | 70 | 37 | 71 73 75 30 54 8.1 57 72 13 27.2 36.2 19 43.2 59 9 74 |

(Appendix 9) strongly suggest parallelism for the derived state of character 9 (in taxa 202 and 203), of character 59 (in taxon 208 with respect to other taxa) and character 74 (in taxa 202 and 204). The single largest compatible clique comprises nine informative characters, 1.1, 8.2, 30, 37, 54, 70, 71, 73 and 75. These support a cladogram that resolves all taxa except 206–8 which remain as a trichotomy. Parsimony analysis yields two equally long minimum length trees which differ in their arrangement of taxa 206–8. There is little biological justification for preferring one or other of these two arrangements (Figs 30, 31) but the larger number of reversals involved in Fig. 31 mitigate marginally in favour of treating taxa 206 and 207 as sister-species.





Figs 30, 31 Alternative cladograms showing most parsimonious arrangement of species of *Euryophion*. Squares indicate autapomorphic developments; circles that an apomorphic feature has been derived in parallel in two separate lineages; diamonds that a feature has undergone three transformations.

All methods of analysis yielded similar results in suggesting that *E. latipennis* and *E. nigripennis* are very closely related, with the former possibly the ancestor of the latter. *E. meridionalis* was always placed on the sister-species to the clade *latipennis* + *nigripennis*, and these three taxa formed a rather distinct species-group. The three taxa whose interrelationship is difficult to resolve, *E. variegatus*, *E. vexatious* and *E. pisinnus*, form a very distinct clade whilst *E. ikuthana* and *E. adustus* are less closely related. Clearly it would be unsatisfactory to place *ikuthana* in a separate genus without at least creating separate genera for the *variegatus* species-group and the *latipennis* species-group. *E. adustus* could be incorporated into the former or also treated as a separate genus. As these insects are essentially similar animals that form a distinct group with respect to other ophiionines, it is suggested that they be placed in a single genus, *Euryophion*, but to represent the phylogeny of the group four species-groups may be recognized. The formal classification may thus be summarized as follows.

EURYOPHION Cameron
Rictophion Townes
latipennis species-group
latipennis (Kirby)
nigripennis Cameron
meridionalis (Morley)
ikuthana species-group
ikuthana (Kriechbaumer)
adustus species-group
adustus (Townes)
variegatus species-group
variegatus Gauld & Mitchell
pisinnus Gauld & Mitchell
vexatious Gauld & Mitchell

Euryophion is primarily an Afrotropical genus with one species, *E. vexatious*, inhabiting southern India (Gauld & Mitchell, 1978; 1981). This taxon is one of the most derived in the genus, and it is very closely related to two African species. This suggests that *Euryophion* may only have recently become established in the Oriental region. The data strongly suggest an African origin for the genus.

RHYNCHOPHION Enderlein

Rhynchophion Enderlein, 1912: 630. Type-species: *Rhynchophion odontandroplax* Enderlein, by original designation.

Mandibles stout, not twisted, barely narrowed distally, with lower tooth somewhat longer than the upper; outer mandibular surface more or less flat, with scattered hairs. Maxillary palp 5-segmented, labial palp 4-segmented; maxilla and labium elongate, projecting below apex of clypeus by about a distance equal to half the length of the head; clypeus in profile flat, with margin often slightly out-flared, in anterior aspect with median obtuse point. Ocelli small, the hind ones separated from the eye by at least their own diameter; frontal carina absent or present but weak; occipital carina complete, ventrally not joining hypostomal carina. Antennae short and stout, not as long as fore wing, and centrally with segments transverse. Pronotum unspecialized; spiracular sclerite exposed; notauli obsolescent; epicnemial carina present only ventrally, not extending onto mesopleuron; mesopleural furrow weakly impressed, horizontal. Scutellum convex, laterally carinate only at extreme anterior end; posterior transverse carina of mesosternum present only laterally as vestiges. Propodeum with anterior area short, present as a deep transverse groove; propodeal carinae absent or with lateral longitudinal ones present as vestiges posteriorly; posterior area convex, rugose-reticulate grading to punctate. Fore wing with pterostigma very slender; marginal cell quite short; *Rs*+*2r* slightly bowed proximally, barely widened near pterostigma; discosubmarginal cell uniformly hirsute; *1m-cu* fairly evenly curved, without a ramellus. Hind wing with *Rs* very weakly bowed. Fore tibial spur without a membranous flange behind macrotrichial comb; mid and hind trochantelli simple; inner hind tibial spur cylindrical, without a fringe of long close hairs; hind tarsal claw long, weakly curved. Gaster stout; tergite 2 in profile about as deep posteriorly as long, sometimes deeper, with thyridia close to anterior margin; umbo absent; epipleuron up-turned. Ovipositor sheath slender.

Rhynchophion is a small genus restricted to the southern part of the U.S.A. and the Neotropical region. Three species have been described, but these may be variants of a single species. They differ principally in the colour of the wings and antennae.

THYREODON Brullé

Thyreodon Brullé, 1846: 150. Type-species: *Thyreodon cyaneus* Brullé, by subsequent designation, Hooker, 1912: 107.

Athyreodon Ashmead, 1900: 87. Type-species: *Athyreodon thoracicus* Ashmead (= *Ophion atriventris* Cresson), by original designation.

Tipulophion Kriechbaumer, 1901b: 75. Type-species: *Tipulophion gigas* Kriechbaumer (= *Ophion atriventris* Cresson), by monotypy.

Macrophion Szépligeti, 1905: 32. Type-species: *Macrophion ornatus* Szépligeti (= *Ophion atriventris* Cresson), by subsequent designation, Viereck, 1912: 640.

Oleter Shestakov, 1926: 259. Type-species: *Oleter selenaction* Shestakov (= *Thyreodon laticinctus* Cresson), by original designation.

Mandibles not twisted, massive, weakly to moderately narrowed distally, usually fairly evenly bidentate, or with lower tooth slightly the longer; outer mandibular surface flat except for a deep proximal concavity. Maxillary palp 5-segmented, labial palp 4-segmented; clypeus in profile from flat to slightly out-flared ventrally, generally with margin sharp; clypeus in anterior aspect with a median apical tooth. Ocelli usually small, the posterior ones widely separated from the eyes, or in a few species with ocelli very large, almost contiguous with eyes; frontal carina present, often very strong; frons medially unusual in many species in being quite strongly raised between the antennal bases; occipital carina present, usually complete, sometimes not reaching hypostomal carina ventrally. Antennae short and stout, central flagellar segments transverse. Pronotum mediodorsally specialized in having anterior and posterior margins raised to form flanges or transverse crests; spiracular sclerite exposed; notauli often strong, generally extending the entire length of the mesoscutum, frequently with crests across anterior ends; epicnemial carina complete, present on mesopleuron; mesopleural furrow absent. Scutellum rather small, moderately convex, either without lateral carinae, or, at most, with carinae present on anterior 0·4; posterior transverse carina of mesosternum present as lateral and central vestiges. Propodeum highly modified, with central part strongly swollen so anterior part is in a very deep groove, as is the spiracle, and with the metapleuron appearing unusually small; propodeal carinae absent, but usually with postero-dorsal surface of propodeum bearing a deep longitudinal concavity; posterior area otherwise from almost smooth to very strongly reticulate. Fore wing with pterostigma slender; marginal cell from short to moderately long; R_s+2r usually only slightly curved and weakly broadened before joining pterostigma; discosubmarginal cell without a glabrous area anteriorly; $1m-cu$ usually evenly curved, without a ramellus. Hind wing with R_s more or less straight. Fore tibial spur without a membranous flange behind the macrotrichial comb; mid and hind trochantelli simple; inner hind tibial spur cylindrical, without a pronounced marginal fringe of long close hairs; hind tarsal claws long and weakly curved. Gaster from moderately stout to long and slender; tergite 2 in profile from slightly to very elongate, with thyridia widely separated from anterior margin; umbo absent; epipleuron pendant, but often creased anteriorly. Ovipositor sheath slender.

Thyreodon is a New World genus with about 25 described species. The majority are diurnally active, and frequently seen feeding from flowers. These species are generally black or brightly coloured, and have small ocelli whereas a few nocturnal species are predominantly brown and have large ocelli. It is perhaps an interesting behavioural 'hangover' from their nocturnal ancestry, that predominantly diurnal species are quite frequently nocturnally active as well and are taken at light.

The centre of diversity of the genus appears to be in northern South America. One species extends as far north as Canada.

The ENICOSPILUS genus-group

This is the largest genus-group in the subfamily, containing both the greatest number of genera and species; it also contains some of the most morphologically specialized of all ophionines. The 14 genera in this group can be divided into five subgroups (the *Orientospilus*, *Ophiogastrella*, *Stauropoctonus*, *Leptophion* and *Enicospilus* subgroups) which correspond with the main evolutionary lineages apparent in the group. The holophyly of this group is supported by a single apomorphy, the loss of the vestigial first laterotergites, which is not a particularly convincing reason for uniting the component genera. However, all share a number of other features, including the complete atrophy of the flange on the fore tibial spur, though this feature is shared with the *Thyreodon* genus-group. It is possible that the *Enicospilus* group may be paraphyletic with respect to the *Thyreodon* group but this relationship could not be resolved further with the

characters and material at hand. The majority of genera in this group (that is the *Stauropoctonus*, *Leptophion* and *Enicospilus* subgroups) clearly constitute a holophyletic group (see Fig. 19); the *Ophiogastrella* subgroup would seem to be the sister-lineage to these. The position of the *Orientospilus* subgroup is less clear, but it seems reasonably placed as the most primitive extant lineage of the group.

This genus-group is primarily a Pan-tropical complex of genera. Only isolated species of *Simophion*, *Stauropoctonus*, *Dicamptus* and *Enicospilus* occur in the Holarctic region. The hosts of the majority of species appear to be tree- and shrub-feeding lepidopterous larvae, though only a small percentage of all the species has been reared.

The *ORIENTOSPILUS* subgroup

This group contains three genera, *Orientospilus*, *Simophion* and *Prethophion*. The systematic position of the latter genus is far from clear as it is united with *Orientospilus* and *Simophion* solely on the basis of a weak character – an incomplete posterior transverse carina of the mesosternum – and its present position is really only the most parsimonious possible. *Prethophion* does share certain features with *Thyreodon* – it has a slightly twisted mandibular axis, though not as pronounced as that of species in the *Thyreodon* lineage, and a similarly stout gaster; like species of the *Thyreodon* lineage the anterior margin of the tegula is not reflexed (possibly a derived feature). However, the plesiomorphic form of the anterior part of the propodeum and tarsal claws seem to exclude *Prethophion* from the *Thyreodon* group as here defined. Furthermore, the first laterotergite is lost and the mandibles are specialized in a quite different way, and much more closely resemble the derived form found in *Orientospilus*.

Simophion and *Orientospilus* are more convincingly related; both have a similarly modified clypeus, have a basally angulate $Rs+2r$ in the fore wing, have lost the epicnemial carina laterally and have a short marginal cell.

ORIENTOSPILUS Morley

Orientospilus Morley, 1912: 6. Type-species: *Orientospilus individuus* Morley, by subsequent designation, Morley, 1913: 378.

Mandibles not twisted, long, strongly and evenly tapered, with upper tooth much longer than the lower; outer mandibular surface flat, sparsely hirsute. Maxillary palp 5-segmented, labial palp 4-segmented; clypeus in profile flat with margin out-flared; in anterior aspect concave. Ocelli moderately large, the posterior ones separated from the eyes by 0.3–1.3 times their minimum diameter; frontal carina absent; occipital carina complete, though ventrally not reaching hypostomal carina. Antennae moderately stout, the distal segments quadrate, the flagellum barely longer than the fore wing. Pronotum mediodorsally with anterior and posterior margins reflexed, raised as keels; spiracular sclerite exposed; notauli absent; epicnemial carina present ventrally, not reaching above level of lower corner of pronotum; mesopleural furrow vestigial or absent. Scutellum quadrate, weakly to moderately convex, with lateral longitudinal carinae complete; posterior transverse carina of mesosternum present only laterally as vestiges. Propodeum with anterior area short, deeply impressed as groove; anterior transverse carina from complete to obsolescent, other carinae absent; posterior area coarsely reticulate, usually medially concave. Fore wing with pterostigma of moderate breadth, evenly narrowed distally; marginal cell short; $Rs+2r$ curved and broadened before joining pterostigma; discosubmarginal cell with a glabrous area anteriorly; $1m-cu$ evenly arcuate without a ramellus. Hind wing with Rs from virtually straight to curved abruptly proximally. Fore tibial spur without a membranous flange behind macrotrichial comb; mid and hind trochantelli unspecialized; hind inner tibial spur more or less flattened, with margin of long close hairs; hind tarsal claw unspecialized. Gaster slender; tergite 2 in profile elongate, with thyridia obsolescent, or if discernible, small and quite close to anterior margin; umbo present; epipleuron usually up-turned, rarely, in some individuals, the posterior part is pendant. Ovipositor sheath slender.

This small genus contains three described species, *capitatus* Gauld & Mitchell from southern and west Africa, *melasma* Townes from Madagascar and *individuus* Morley from eastern peninsular India. Structurally these are very similar insects. The Madagascan species is the least specialized; both the Indian and African species have lost the anterior transverse carina of the propodeum and have a shorter, stouter and apically more setaceous flagellum and have a broader malar space suggesting they are sister-species (Fig. 32). The Madagascan species may well be the ancestor of the other two.

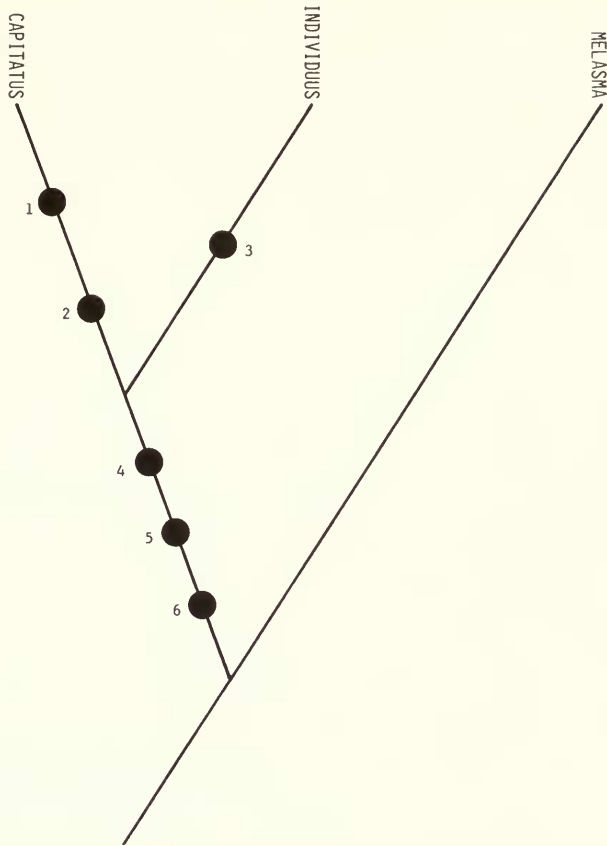


Fig. 32 Putative phylogenetic arrangement of species of *Orientospilus*. This cladogram is supported by the following apomorphic features: 1, malar space very wide; 2, ocelli widely separated from eyes; 3, *Rs* in hind wing curved proximally; 4, flagellum with proximal segments almost quadrate; 5, anterior transverse carina of propodeum absent; 6, malar space moderately wide, at least 0.4 times basal mandibular width.

PRETHOPHION Townes

Prethophion Townes, 1971: 74. Type-species: *Prethophion latus* Townes, by original designation.

Mandibles very slightly twisted, very strongly narrowed, subequally bidentate; outer mandibular surface slightly convex, with a proximal concavity. Maxillary palp 5-segmented, labial palp 4-segmented; clypeus in profile almost flat, margin centrally blunt, clypeus in anterior aspect virtually almost truncate. Ocelli large, the posterior ones more or less touching eyes; frontal carina absent; occipital carina entirely absent. Antennae moderately slender, barely longer than fore wing but with central segments clearly elongate. Pronotum unspecialized; spiracular sclerite exposed; notauli vestigial; epicnemial carina present on mesosternum, present but very weak on mesopleuron; mesopleural furrow very distinct, oblique, extending from episternal scrobe to subalar prominence, the speculum posterodorsal to this carina strongly inflated. Scutellum convex, laterally carinate only on extreme anterior end; posterior transverse carina of mesosternum absent except for lateral vestiges. Propodeum short and abruptly declivous posteriorly; anterior area unspecialized; anterior transverse carina complete; blunt tubercles (which are possibly vestiges of posterior transverse carina) discernible; posterior area concave, very finely alutaceous. Fore wing with pterostigma moderately slender; marginal cell slender; *Rs*+*2r* proximally not broadened, almost straight; discosubmarginal cell without a glabrous area anteriorly; *1m-cu* fairly evenly curved, without a ramellus. Hind wing with *Rs* strongly curved. Fore tibial spur without a membranous flange behind macrotrichial comb; mid and hind trochantelli not specialized; inner hind tibial spur flattened, with a margin of long close hairs; hind tarsal claw unspecialized. Gaster quite stout, centrally almost cylindrical;

tergite 2 in profile elongate, with thyridia close to anterior margin; umbo low but distinct; epipleuron up-turned. Ovipositor sheath stout.

This enigmatic genus contains a single species which occurs at low altitudes in Peru and Bolivia. Nothing is known of its biology.

SIMOPHION Cushman

Simophion Cushman, 1947: 446. Type-species: *Simophion excarinatus* Cushman, by original designation.

Mandibles fairly evenly tapered, not or barely twisted, subequally bidentate or with lower tooth slightly the shorter; outer mandibular surface punctate, proximally concave. Maxillary palp 5-segmented, labial palp 4-segmented; clypeus in profile flat, apically sometimes slightly out-flared, in anterior aspect concave. Ocelli moderately large, the posterior ones separated from eye by 0.2–0.7 times their maximum diameter; frontal carina absent; occipital carina complete, though generally not reaching hypostomal carina ventrally. Antennae moderately long and slender, about 1.4–1.6 times length of fore wing. Pronotum unspecialized; spiracular sclerite exposed; notauli vestigial; epicnemial carina present ventrally, not reaching onto mesopleuron laterally; mesopleural furrow weak, diagonal, extending from episternal scrobe to near subalar prominence. Scutellum moderately convex, narrow, without lateral carinae; posterior transverse carina of mesosternum present only laterally as vestiges. Propodeum with anterior area short, striate slightly centrally; anterior transverse carina absent as are other propodeal carinae, the propodeum being narrowed distally; marginal cell short; *Rs*+2*r* very abruptly angled before joining pterostigma, its extreme end abruptly broadened; discosubmarginal cell very sparsely hirsute, with a glabrous area anteriorly; *1m-cu* curved or sinuous, without a ramellus. Hind wing with *Rs* very strongly bowed. Fore tibial spur without a membranous flange behind macrotrichial comb; mid and hind trochantelli unspecialized; inner hind tibial spur flattened, with a margin of long hairs; hind tarsal claws unspecialized. Gaster slender; tergite 2 in profile elongate, with thyridia obsolescent, or if present quite large and relatively close to anterior margin of tergite; umbo distinct; epipleuron up-turned. Ovipositor sheath slender.

This moderately small genus is restricted to the 'Mediterranean' type biomes of the northern hemisphere. Two species occur in the Middle East and Central Asia (Horstmann, 1981), whilst five or six occur in the south-west of the United States (Townes, 1971). Similar disjunct distributions occur in several genera of lower Aculeata (M. C. Day, pers. comm.) and in the myrmicine ant genus *Messor* (Bolton, 1982). Amongst ophiionines *Eremotylus* has a similar, though slightly more extensive distribution.

The *OPHIOGASTRELLA* subgroup

This group comprises a single Neotropical genus, *Ophiogastrella*, which was treated as a member of the *Ophion* genus-group by Cushman (1947), but as a member of the Enicospilini by Townes (1971). Townes & Townes (1973) considered it to be closely related to *Laticoleus*.

Structurally *Ophiogastrella* shows a remarkable combination of primitive and derived features. The specialized fore tibial spur and first laterotergite suggest it belongs close to the base of the *Enicospilus* lineage, but the well-developed umbo, exposed spiracular sclerite and unspecialized anterior part of the propodeum suggest it is more primitive than many other genera. These features, together with the lack of an impressed clypeal apex, externally flat mandible and slender ovipositor sheath suggest it is not at all closely related to *Laticoleus*. The peculiar male claws are an autapomorphy of this taxon.

Ophiogastrella is confined to the southern part of Central America and northern South America. There is no evidence to suggest the group has ever occurred elsewhere.

OPHIOGASTRELLA Brues

Ophiogastrella Brues, 1912: 201. Type-species: *Ophiogastrella maculithorax* Brues, by original designation.

Brachyscения Enderlein, 1921: 36. Type-species: *Brachyscения nigriventris* Enderlein, by original designation.

Mandibles not twisted, evenly but only moderately narrowed apically, subequally bidentate; outer mandibular surface flat except for small proximal concavity, centrally with scattered hairs. Maxillary palp 5-segmented; labial palp 4-segmented; clypeus in profile flat or weakly convex, margin blunt or sharp, never impressed; clypeus in anterior aspect weakly convex, straight or very slightly concave. Ocelli large, the posterior ones generally very close to the eyes; frontal carina absent; occipital carina complete, ventrally (as genal carina) usually sharply angled and complete to hypostomal carina. Antennae of

moderate length, 1.2–1.5 times the length of the fore wing, rarely slightly longer. Pronotum unspecialized; spiracular sclerite exposed; notauli absent; epicnemial carina complete; mesopleural furrow absent or weakly impressed, diagonal, extending from episternal scrobe to near subalar prominence. Scutellum weakly to moderately convex, with lateral longitudinal carina extending about 0.8 of its length; posterior transverse carina of the mesosternum vestigial. Propodeum with anterior area short, unspecialized; anterior transverse carina from complete to absent, other carinae at most present only as vestiges; posterior part of propodeum generally rather smooth. Fore wing with pterostigma quite large and broad; marginal cell long; $Rs+2r$ curved or slightly angled proximally, from slender to moderately broadened; discosubmarginal cell with a small glabrous area anteriorly; $1m-cu$ very strongly and evenly curved, without a ramellus. Hind wing with Rs from almost straight to strongly bowed. Fore tibial spur without a membranous flange behind the macrotrichial comb; mid and hind trochantelli simple or with a blunt tooth near distal margin; inner hind tibial spur flattened, with a fringe of close hairs; hind tarsal claws of female unspecialized, of male flattened with pectinal comb present on both sides (Fig. 47). Gaster moderately slender; tergite 2 in profile elongate, with thyridia remote from anterior margin; umbo quite well developed; epipleuron generally upturned. Ovipositor sheath slender.

Ophiogastrella is a small genus containing about 10 species, of which only three are described (Townes & Townes, 1966). They are restricted to the Neotropical region from Costa Rica to about 10°S in Brazil, and seem to be associated with areas which have a pronounced dry season.

The species are rather similar to each other, and best separated by differences in the length of $3r-m$, shape of Rs in the hind wing and sculpture of the propodeum. There are also more subtle differences in the shape of the clypeus, and the head.

The *STAUROPOCTONUS* subgroup

This subgroup contains two genera, *Stauropoctonus* (including as a synonym *Aulophion*) and *Lepiscelus*. The exposed spiracular sclerites of species in this complex suggest it is one of the more primitive of enicospiline lineages. It is also one of the taxonomically most distinctive as its members are characterized by an incomplete occipital carina, a transverse mesopleural furrow, slender pterostigma, basally thickened and bent $Rs+2r$ and a very sinuous $1m-cu$. Most species have $1m-cu$ and Cu_{1a} basally widely separated, and all have the mid and hind trochantelli specialized.

The group contains few species. The most primitive *Stauropoctonus* species and the solitary *Lepiscelus* occur in the Old World, suggesting an Old World origin for the group.

LEPISCELUS Townes

Lepiscelus Townes, 1971: 73. Type-species: *Lepiscelus gracile* Townes (= *Eremotylus distans* Seyrig), by original designation.

Mandibles twisted about 5°, proximally strongly narrowed, distally parallel-sided with upper tooth about twice as long as the lower; outer mandibular surface more or less flat. Maxillary palp 5-segmented, labial palp 4-segmented; clypeus in profile weakly convex, margin narrowly acute, laterally blunted, short, exposing labrum; clypeus in anterior aspect truncate or even slightly concave. Ocelli large, the hind ones very close to the eyes; frontal carina absent; occipital carina entirely absent. Antennae very long and slender, about 1.7 times length of the fore wing. Pronotum mediodorsally rather long, flat; spiracular sclerite exposed; notauli very short but often strongly impressed in part; epicnemial carina weak, laterally becoming obsolete at level of lower corner of pronotum; mesopleural furrow very weakly impressed, transverse. Scutellum almost rectangular, carinate laterally only at extreme anterior end; posterior transverse carina of mesosternum complete. Propodeum with anterior area moderately long, dorsally without carinae, with posterior area finely wrinkled to rugulose. Fore wing with pterostigma slender; marginal cell long; $Rs+2r$ abruptly curved and broadened before joining pterostigma; discosubmarginal cell anteriorly glabrous; $1m-cu$ very strongly sinuate. Hind wing with Rs strongly curved; hamuli arranged in two groups, the proximal group comprising two which are longer and flatter than those in the distal group of three. Fore tibial spur without a membranous flange behind the macrotrichial comb; mid and hind trochantelli extended apically as a broad flange over the proximal end of the femur; inner hind tibial spur flattened, with a margin of long, close hairs; hind tarsal claws quite long, those of male more closely pectinate than those of the female. Gaster slender; tergite 2 in profile elongate, with thyridia remote from anterior end; umbo vestigial; epipleuron up-turned. Ovipositor sheath slender; male with gonosquama unusually long.

Lepiscelus contains a single species which is widespread, but apparently rather uncommon, throughout the Afrotropical region between latitude 10°N and 20°S. The most distinctive feature of this genus is the

flanged mid and hind trochantelli which are, amongst the Ichneumonidae, a unique feature of *Lepiscelus distans*. Nothing is known of the biology of this insect, but the form of the mandibles and head shape are reminiscent of some species of *Enicospilus* that either inhabit arid areas or are active in the dry season.

STAUROPOCTONUS Brauns

Stauropoctonus Brauns, 1889: 75. Type-species: *Ophion bombycivorus* Gravenhorst, by monotypy.
Stauropodoctonus Morley, 1913: 375. [Unjustified emendation.]

Nipponophion Uchida, 1928: 201. Type-species: *Nipponophion variegatus* Uchida (= *Ophion bombycivorus* Gravenhorst), by monotypy.

Aulophion Cushman, 1947: 458. Type-species: *Aulophion bicarinatus* Cushman, by original designation.
 Syn. n.

Mandibles twisted about 85°, evenly, but quite strongly narrowed apically, subequally bidentate. Maxillary palp 5-segmented, labial palp 4-segmented; clypeus in profile weakly convex, in anterior aspect with margin slightly convex. Ocelli large, the posterior ones close to eye margins; frontal carina absent; occipital carina usually absent, partially present in one species. Antennae very long and slender, sometimes up to 2 times length of fore wing. Pronotum unspecialized, spiracular sclerite exposed; notauli vestigial or absent; epicnemial carina from present and complete to absent; mesopleural furrow strong, extending from episternal scrobe to upper end of prepectal carina (or the corresponding position if this carina is absent), in some species impressed as a deep groove. Scutellum moderately convex to convex, either without lateral carinae or with carina incomplete; posterior transverse carina of mesosternum from complete to reduced to lateral vestiges. Propodeum with anterior area long; anterior transverse carina usually complete, the posterior one sometimes discernible; posterior area from weakly rugulose to reticulate. Fore wing with pterostigma moderately slender; marginal cell long; *Rs+2r* abruptly curved and slightly thickened basally; discosubmarginal cell with a glabrous area anteriorly, which may be expanded along *Rs+2r*; *1m-cu* without a ramellus, either evenly bowed or sinuous. Hind wing with *Rs* from almost straight to weakly bowed. Fore tibial spur without a membranous flange behind macrotrichial comb; mid and hind trochantelli specialized in having the outer distal margin produced into a strongly decurved sharp spine; inner hind tibial spur flattened, with a marginal fringe of long hairs; hind tarsal claws unspecialized. Gaster slender; tergite 2 in profile very elongate, with the thyridia remote from anterior margin; umbo vestigial; epipleuron pendant or up-turned. Ovipositor sheath slender.

In the analysis of the genera *Stauropoctonus* appeared to be paraphyletic with respect to *Aulophion*. The latter genus has been separated from *Stauropoctonus* by possession of two apomorphic features (Cushman, 1947; Townes, 1971). No apomorphies have ever been suggested for *Stauropoctonus*, though the clade *Stauropoctonus* + *Aulophion* is one of the most clearly defined in the subfamily. It is characterized by the following combination of apomorphies (though none is actually unique to the clade) – at least partial loss of occipital carina; presence of projections on mid and hind trochantelli; presence of impressed transverse furrow on mesopleuron; presence of strongly twisted mandibles; having *Rs+2r* in the fore wing basally angled. In addition to these features the head and mesoscutal profile of species of this clade are characteristic, though these ‘apomorphies’ are so subtle I have not been able to code them. To further resolve the relationship between *Aulophion* and *Stauropoctonus* more data were analysed.

The following taxa were included – *Aulophion* sp. 1 (? *bicarinatus*) (301), *Aulophion* sp. 2 (302), *Stauropoctonus bombycivorus* (303), *S. torresi* (304), *S. townesorum* (305) and *S. occipitalis* (306). This is all the species in the group except for one (or possibly two) *Aulophion* species which are very closely related to taxon 302. To represent the range of interspecific variation in the group the following characters from the primary set were utilized – 1·2, 19, 20·1, 24·1, 25·2, 27, 30, 36, 43·1, 43·2, 44·1, 45·2, 47·2, 57 and 59. (It is noteworthy that 27 and 36 are composites of 27·1 and 27·2 and 36·1 and 36·2 respectively; these characters showed identical state distribution over the data and therefore were treated as single characters to avoid excess weighting.) In addition to these fifteen, three further characters were used.

- 80 Median carina of propodeum. This apomorphic feature (1) is found only in a few isolated Neotropical ophionines. The plesiomorphic condition, no median carina, is found in virtually all ophionines and members of the various out-groups.
- 81 Metapleural sculpture. In most out-group taxa, most ophionines and several species of this group the metapleuron is smooth and finely punctate. Some *Stauropoctonus* species are specialized in having this region coarsely rugose (1).
- 82 Position of *cu-a* with respect to *Rs&M* in fore wing. The plesiomorphic condition for ophionines apparently is for *cu-a* to be proximal to the base of *Rs&M*. A few *Stauropoctonus* are specialized in having these veins opposite (1).

Table 22 Primary data matrix for genus *Stauropactonus*. The taxa corresponding to the numbers are given in the text (p. 146).

| | 1.2 | 20.1 | 25.2 | 30 | 43.1 | 44.1 | 47.2 | 59 | 81 | | |
|-----|-----|------|------|----|------|------|------|----|----|----|---|
| | | 19 | 24.1 | 27 | 36 | 43.2 | 45.2 | 57 | 80 | 82 | |
| 301 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 |
| 302 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 |
| 303 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 |
| 304 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 |
| 305 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 |
| 306 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |

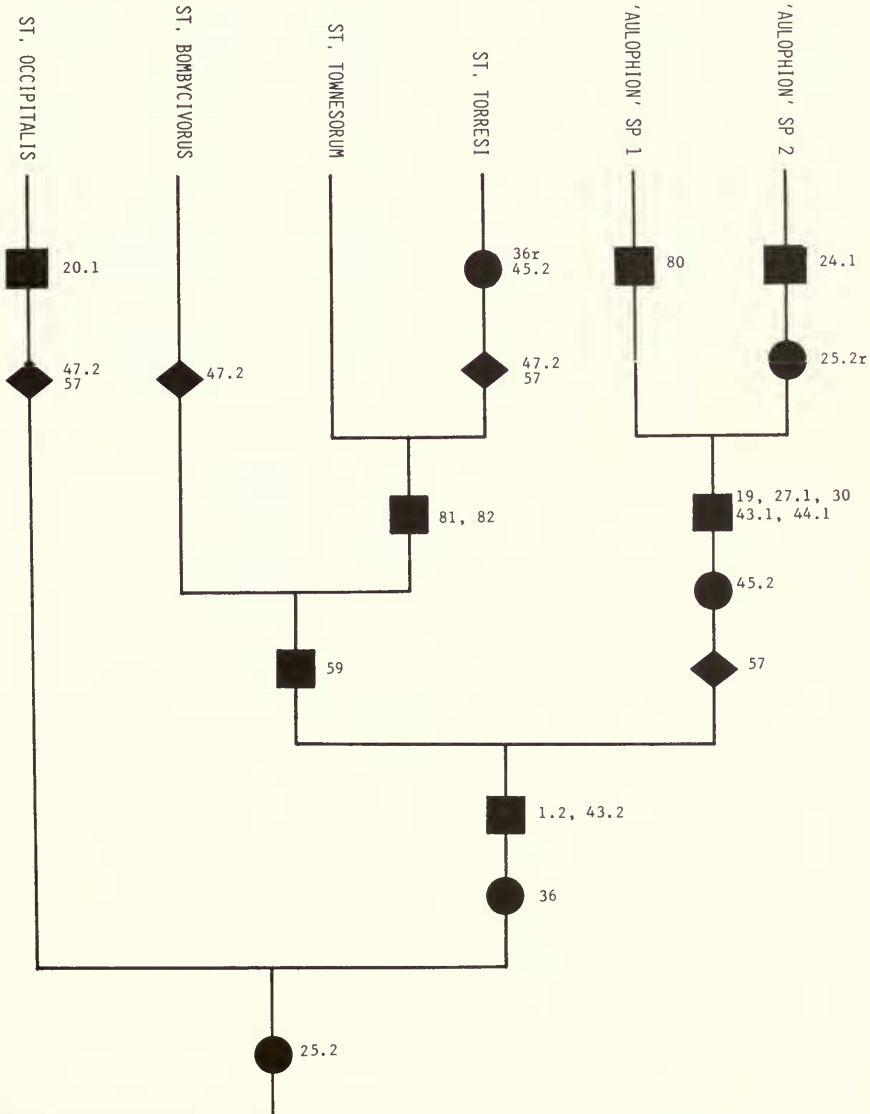


Fig. 33 Favoured cladogram showing putative phylogenetic arrangement of species of *Stauropactonus*. This is based on the largest compatible set of ten informative characters and requires 25 transformation steps.

The primary data matrix for taxa 301–6 is shown in Table 22. Parsimony and compatibility analyses, using techniques outlined above, yielded two 'best' alternative hypotheses of phylogenetic relationship (Figs 33, 34). The cladograms have a large number of features in common. Firstly, both suggest *Stauropoctonus* is paraphyletic with respect to *Aulophion*, and this in turn suggests that *Aulophion* can be treated as a synonym of *Stauropoctonus*, as has been formally proposed above. Secondly, both suggest that

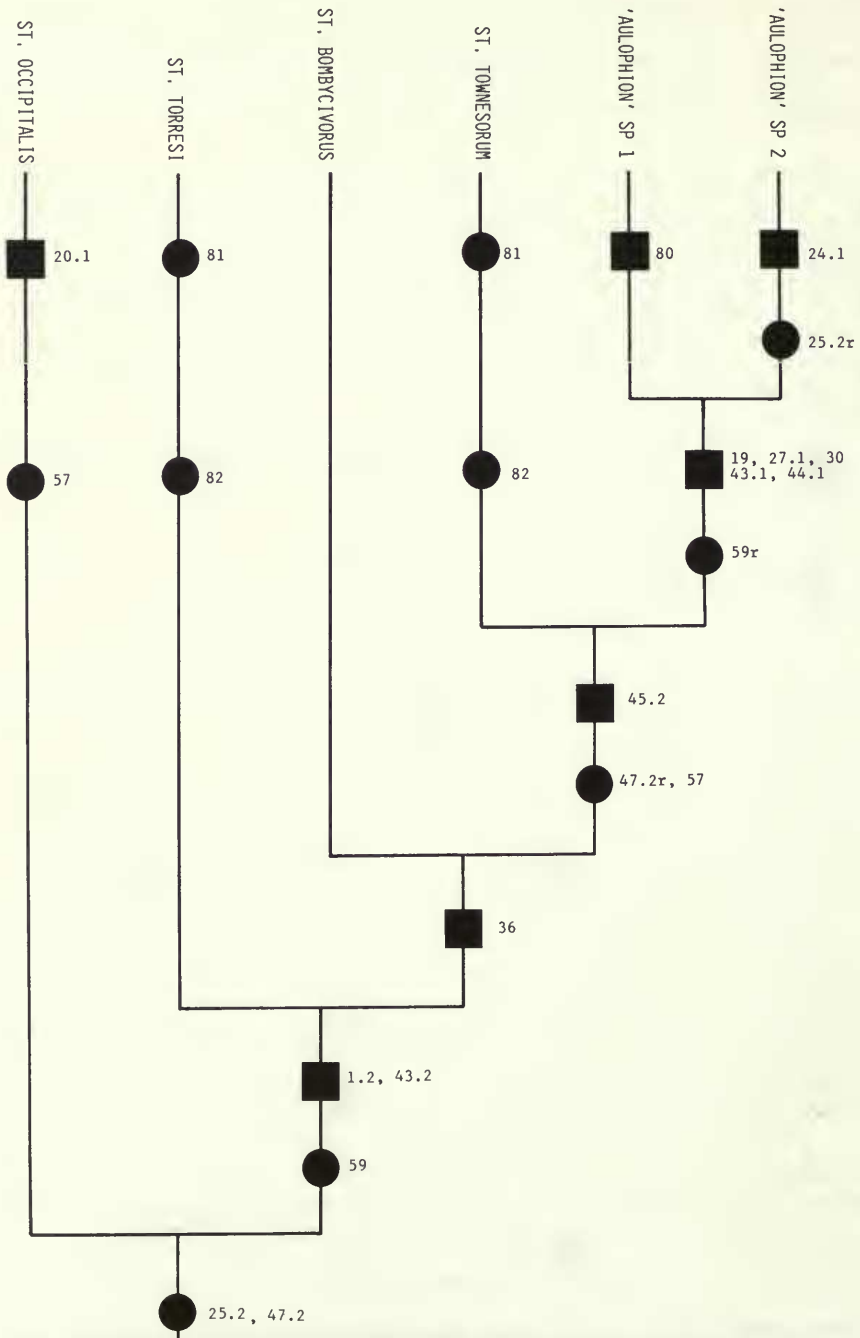


Fig. 34 Alternative cladogram for species of *Stauropoctonus*. This is the most parsimonious arrangement of taxa discovered and requires 24 transformation steps. (Symbols as for Figs 30–31.)

Aulophion is both a holophyletic clade and the most derived lineage in the group. Thirdly, both place *S. occipitalis* as the most primitive taxon in the group. The two cladograms differ in their arrangement of *S. bombycivorus*, *S. torresi* and *S. townesorum* and these different arrangements depend on the alternative compatible sets of characters 36 and 45·2 versus 59, 81 and 82. Character 36 has been demonstrated to be both unreliable and of dubious polarity, whilst 45·2 can be regarded as a loss apomorphy (loss of hairs on wing membrane). Character 59 (colour of interocellar area) is also far from a convincing apomorphy, but 81 and 82 strongly suggest that *torresi* and *townesorum* are sister-species. *S. bombycivorus* is rather difficult to place, but could be either the ancestor of, or a close relative of the ancestor of both the '*Aulophion*' species-group and *torresitownesorum*.

The more primitive species of this genus (*occipitalis* and *bombycivorus*) are restricted to the Old World, the former to the mountains of Madagascar and the latter to the southern part of the Palaearctic, except in Asia where it extends north into Kamchatka and the Kurile Islands (Townes, Momoi & Townes, 1965). Possibly the ancestor of these taxa was widely distributed in the Old World at one time, and the Madagascan survivor is a relict of this. There are clear indications in the Madagascan fauna of an ancient Palaearctic affinity amongst the Hymenoptera. The symphytan taxon Cephidae is represented on the island and in the Holarctic only (Benson, 1935), and a number of ichneumonid genera have rather similar distributions, e.g. *Neliopisthus*, *Euceros* (Townes, 1969; Barron, 1978). As the widespread Palaearctic species *bombycivorus* may be almost directly ancestral to the two other species-groups, it may at one time have also occurred in the Nearctic region. The *torresitownesorum* group is Malasian/Melanesian, with the former species constituting part of the characteristically intrusive, Indo-Papuan faunal element in northern Australia (Gauld, 1984a). The distribution of *torresi*, in transcending both Wallace's and Weber's lines, suggests its current range is the result of a dispersive rather than a vicariance event. The Neotropical species form a rather distinctive clade. The most northerly extent of their distribution seems to be Costa Rica where one species occurs in lower montane (1000–1500 m) forest, whilst none has been found south of 25°S. Perhaps the ancestor of this group reached South America from the north during the Miocene when an archipelagic connection existed between the two continents (Rich & Rich, 1983). This evolutionary 'scenario' is based on the supposition that a *Stauropogon* occurred in the United States. At present there is no evidence for this; the scenario presented is merely the most parsimonious interpretation of data. Other scenarios would necessitate advocating much more widespread extinction.

The LEPTOPHION subgroup

This complex of genera is characterized by the form of the mandibles, which have a more or less discernible impressed groove extending diagonally, the convex clypeus with an impressed acute margin, the very long slender antennae and, for most species, a somewhat broadened ovipositor sheath. The venation of all species is rather similar in having *Rs+2r* basally broadened, and often angulate before joining the pterostigma; *1m-cu* is either sinuate or evenly curved.

This subgroup contains three genera, *Leptophion*, *Laticoleus* and *Pamophion* which are difficult to resolve as the holophyly of *Leptophion* cannot convincingly be demonstrated. *Pamophion*, a monobasic taxon, is holophyletic and is apparently the sister-lineage of *Leptophion* + *Laticoleus*. The latter is a holophyletic group, but it may have arisen from within the former. The only apomorphy that can be postulated for *Leptophion* is the presence of a specialized penultimate hamulus. (The apomorphies shown in Fig. 19 are subject to much exception and parallelism in some species of *Laticoleus*, and reference to the overall classification suggests that presence of a complete posterior transverse carina of the mesosternum is plesiomorphic for this complex – though some taxa have partially lost this carina.) The assumption that the specialized hamulus is a group apomorphy necessitates speculating that reversal has occurred in several taxa, but there is some evidence that this has happened. For example, *L. tetus* has a slight indication of some enlargement of the hamulus and its sister-species, *L. yampus*, has it clearly specialized, though not as large as that of *L. iochus*, the sister-species of *yampus* + *tetus*. *L. ankylosus* and *L. eithos* are highly specialized species (without a modified hamulus) which are closely related to *L. vernalis* which has a long penultimate hamulus, and *Leptophion* species 1 (BMNH) which has it only slightly modified. These four species apparently belong to the *maculipennis* lineage, the remainder of which all have a highly specialized hamulus. A tentative phylogeny for this subgroup is proposed in Fig. 35. *Laticoleus* is retained as a separate genus, but its validity needs to be reassessed as more material becomes available for study and the phylogeny of the species of *Leptophion* is better understood.

Judging from the present distribution of this group (Fig. 36) it is most parsimonious to postulate an Old World origin for this complex of genera. The more primitive taxa are restricted to Melanesia or Australia which suggests an Australo-Melanesian origin for this group. However, if *Laticoleus* is truly primitive with respect to *Leptophion*, then an alternative hypothesis is that this group was once widely spread in the Old

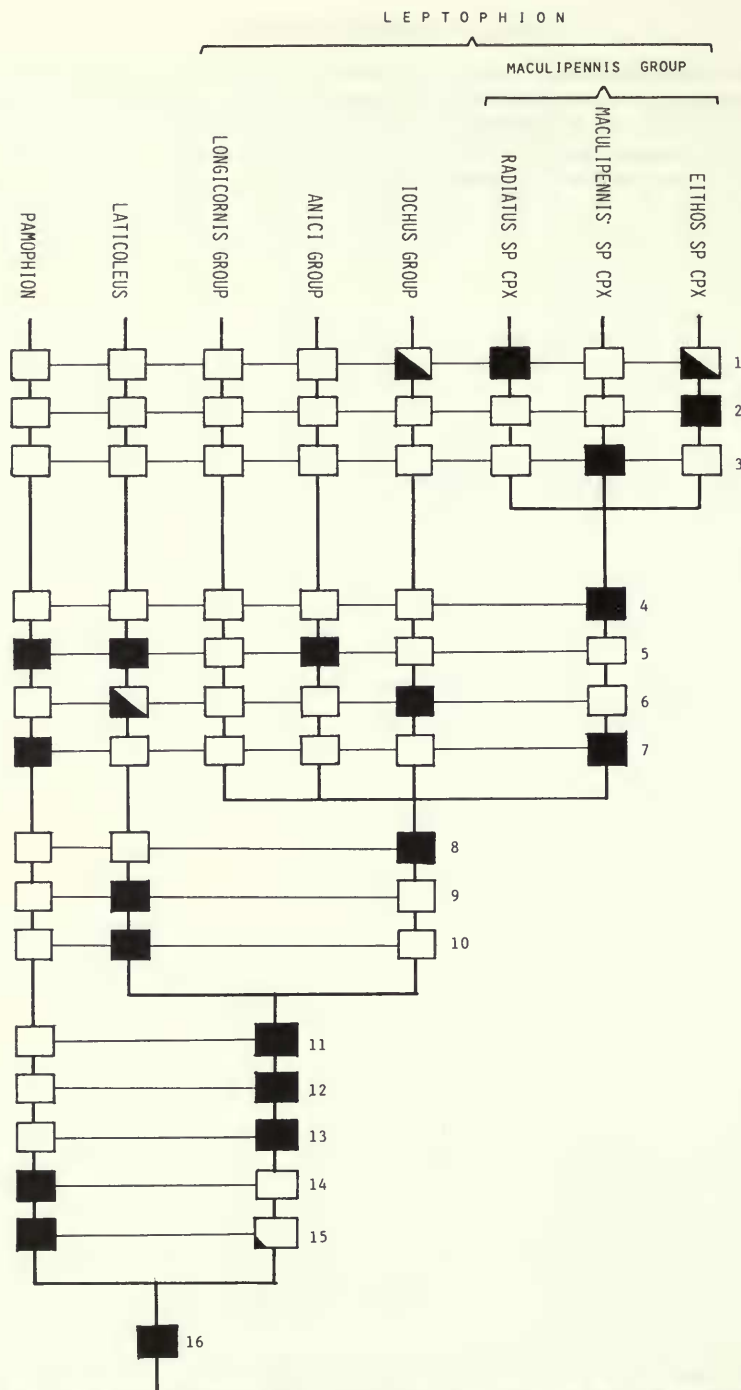


Fig. 35 Cladogram showing putative phylogeny of groups of species in the *Leptophion* subgroup. Black squares represent apomorphic features, white plesiomorphic; diagonally divided squares indicate a mixture of the two states in the component species of a particular lineage. The characters that support this arrangement are: 1, loss of specialized hamulus; 2, R_s+2r emitted from centre of pterostigma; 3, $1m-cu$ very sinuous; 4, specialized hind tarsal claws; 5, loss of posterior transverse carina of mesosternum; 6, presence of a 'hair brush' on mandible; 7, genal carina evanescent before joining hypostomal carina; 8, lengthened penultimate distal hamulus; 9, exceptional broad ovipositor sheath that in profile is almost quadrate; 10, long malar space; 11, ovipositor sheath at least moderately broad, in profile more than 0.4 times as deep as long; 12, marginal cell of hind wing at least partially glabrous; 13, anterior area of propodeum elongate; 14, epipleuron 2 pendant; 15, hind trochantellus marginally produced into blunt tooth; 16, posterior transverse carina of mesosternum present.

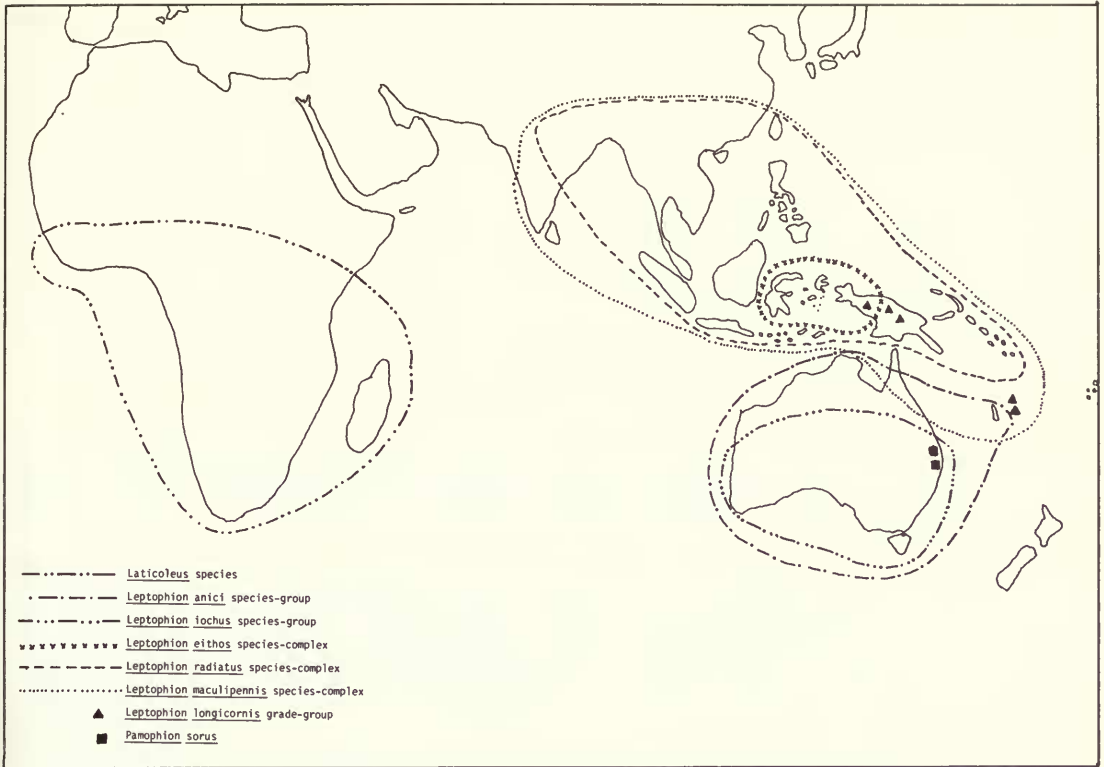


Fig. 36 The geographical distribution of taxa of the *Leptophion* subgroup.

World tropics and has suffered considerable extinction, leaving only a rather specialized primitive lineage in the Afrotropical region and a few relicts east of Wallace's line. Gauld (1984a) suggested that the *anici* and *iochus* groups of *Leptophion*, in Australia, have had a northern origin, and that once their ancestors had adapted sufficiently to cross the rain forest/savannah interface (Taylor, 1972) then they had ample opportunity to give rise to radiations in species-poor Australia (Gauld, 1984a). The most specialized group of *Leptophion*, the *maculipennis* group, is best represented in the more easterly parts of Indonesia and Melanesia. It is probable that this species-group arose in this area and a few species have spread west to the Asian mainland.

LATICOLEUS Townes

Laticoleus Townes, in Townes & Townes, 1973: 358. Type-species: *Coiloneura unicolor* Szépligeti, by original designation.

Mandibles not twisted, weakly narrowed apically, generally subequally bidentate; outer mandibular surface with subbasal swelling weak or well developed, with a diagonal groove extending from the upper proximal corner to between bases of teeth. Maxillary palp 5-segmented, labial palp 4-segmented; clypeus in profile convex, margin impressed, in anterior aspect with margin weakly convex. Ocelli generally moderately large, the posterior ones separated from the eyes by 0.2–1.0 times their minimum diameter; frontal carina absent; occipital carina complete, the lower part (genal carina) reaching to hypostomal carina. Antennae very long and slender, at least 1.5 times length of fore wing. Pronotum usually unspecialized, or in one Madagascan species with anterior margin mediodorsally expanded and curved back; spiracular sclerite partially concealed; notauli vestigial or absent; epicnemial carina complete, weak or even absent on mesopleuron; mesopleural furrow undeveloped. Scutellum weakly convex, with lateral longitudinal carinae present, more or less complete; posterior transverse carina of the mesosternum incomplete, present as lateral or rarely central vestiges. Propodeum with anterior area moderately long, striate or smooth; anterior transverse carina present or absent, other carinae usually absent; posterior area from rugose to virtually smooth. Fore wing with pterostigma moderately stout; marginal cell long; $Rs+2r$

conspicuously thickened near pterostigma, often abruptly curved in proximal part; discosubmarginal cell with a glabrous area in anterior corner, this area generally quite large, and in one species, bearing a weak sclerite; $1m-cu$ without a ramellus, usually fairly evenly bowed, in a few species slightly sinuous. Hind wing with Rs from almost straight to strongly curved, with marginal cell proximally, at least narrowly glabrous; distal hamuli unspecialized, or with proximal three enlarged. Fore tibial spur without a membranous flange behind macrotrichial comb; mid and hind trochantelli unspecialized or with a weak tooth projecting distally; inner hind tibial spur flattened with a margin of close long hairs; hind tarsal claws usually unspecialized, rarely with very coarse pectinae. Gaster slender; tergite 2 in profile very elongate, with thyridia well removed from anterior margin; umbo absent; epipleuron up-turned. Ovipositor sheath exceptionally broad.

Laticoleus is a moderately small Afrotropical genus containing 11 described species (Gauld & Mitchell, 1978). The majority occur in Madagascar and east Africa. Nothing is known of the biology of species of this genus.

LEPTOPHION Cameron

Leptophion Cameron, 1901: 227. Type-species: *Leptophion longiventris* Cameron, by monotypy.

Spilophion Cameron, 1905: 124. Type-species: *Spilophion maculipennis* Cameron, by monotypy.

Coiloneura Szépligeti, 1905: 35. Type-species: *Coiloneura melanostigma* Szépligeti (= *Leptophion longiventris* Cameron), by subsequent designation, Viereck, 1914: 35.

Mandibles not twisted, weakly narrowed apically, generally subequally bidentate; outer mandibular surface often with a basal swelling, and with a diagonal groove extending from near upper corner to between bases of teeth, sometimes with this groove bearing a brush of long hairs, other times with the groove very weak. Maxillary palp 5-segmented, labial palp 4-segmented; clypeus in profile convex, margin impressed acute, in anterior aspect usually with margin weakly convex, rarely slightly concave. Ocelli generally large, the posterior ones close to the margins of the eyes, or rarely in some Australian examples, with ocelli smaller; frontal carina absent; occipital carina either complete or obsolescent at extreme ventral end so the carina fails to join the hypostomal carina. Antennae in most species very long and slender, at least 1.5 times the length of the fore wing, in some Australian species shorter, barely longer than the fore wing. Pronotum unspecialized; spiracular sclerite partially concealed, in a few Malesian taxa almost completely covered; notauli vestigial or absent; epicnemial carina complete; mesopleural furrow usually undeveloped. Scutellum moderately convex, from without lateral carinae to with these carinae complete; posterior transverse carina of mesosternum complete, interrupted before mid coxae, or rarely absent. Propodeum with anterior area long and usually striate; anterior transverse carina usually complete, rarely absent, the other carinae usually not discernible; posterior area from strongly rugose to smooth and shining. Fore wing with pterostigma moderately broad; marginal cell long; $Rs+2r$ conspicuously thickened near pterostigma, usually abruptly curved or angled near base; discosubmarginal cell usually with a glabrous area in anterior corner, this area usually large and extending 0.2 of the way down $Rs+2r$, rarely with a weak alar sclerite, sometimes secondarily with microtrichia obscuring part of glabrous area; $1m-cu$ usually without a ramellus, either evenly bowed or, more usually, sinuous. Hind wing with Rs from almost straight to very strongly bowed, with marginal cell adjacent to this vein at least narrowly glabrous; distal hamuli unspecialized or with penultimate hamulus long and coiled. Fore tibial spur without a membranous flange behind macrotrichial comb; mid and hind trochantelli unspecialized; inner hind tibial spur flattened, with a fringe of long close hairs; hind tarsal claws unspecialized or with distal pectinal tooth projecting beyond the apex of the claw. Gaster usually slender, tergite 2 in profile from moderately to very elongate, with thyridia remote from anterior margin; umbo absent; epipleuron up-turned. Ovipositor sheath moderate, broad.

Leptophion is a moderately large Indo-Pacific genus containing 30 described species (Gauld, 1977; Gauld & Mitchell, 1981). The majority are restricted to lower montane forests on the islands to the east of the Sunda Shelf. Many are endemic to a particular island and recent collecting has yielded an undescribed species from Sulawesi (BMNH). Most species are only known from relatively few individuals.

The genus is divisible into four species-groups, the largest of which, the *maculipennis* species-group, may be subdivided into three species-complexes.

Key to species-groups and complexes of *Leptophion*

- 1 Anterior transverse carina of mesosternum incomplete; propodeum often with anterior transverse carina absent *anici* species-group

- Anterior transverse carina of mesosternum complete; propodeum almost always with anterior transverse carina complete 2
- 2 Hind tarsal claw simple; genal carina usually joining hypostomal carina 3
- Hind tarsal claw with distal pectinal tooth projecting apically; genal carina usually not reaching hypostomal carina (*maculipennis* species-group) 4
- 3 Mandible with a dense brush of long stout hair on outer surface *iochus* species-group
- Mandible with scattered hairs on outer surface *longicornis* grade-group
- 4 Fore wing with $Rs+2r$ emitted from near centre of pterostigma; anterior corner of discosubmarginal cell partially hirsute *eithos* species-complex
- Fore wing with $Rs+2r$ emitted from proximal end of pterostigma; anterior corner of discosubmarginal cell glabrous 5
- 5 Penultimate distal hamulus unspecialized; fore wing with $1m-cu$ from evenly curved to weakly sinuous *radiatus* species-complex
- Penultimate distal hamulus long and coiled; fore wing with $1m-cu$ moderately to strongly sinuous *maculipennis* species-complex

***longicornis* grade-group**

This paraphyletic assemblage contains two species, *L. longicornis* (Szépligeti) and *L. bakeri* (Cheesman). The group can only be characterized by symplesiomorphies. It is restricted to New Guinea and the New Hebrides.

***anici* species-group**

This holophyletic group contains three species, *L. anici* Gauld, *L. antennatus* (Morley) and *L. unicalcaratus* Gauld. The group is characterized by the loss of the posterior transverse carina of the mesosternum; species tend to have less propodeal sculpture than most *Leptophion* species, and usually the transverse carina is lost. The *anici* species-group is restricted to Australia and New Caledonia where species occur in drier habitats than most *Leptophion*.

***iochus* species-group**

This holophyletic group contains three Australian species, *L. iochus* Gauld, *L. yampus* Gauld and the aberrant *L. tetus* Gauld. The group is characterized by possession of a brush of hair on the outer surface of the mandible; they are generally more robust species with more densely pubescent wings than most *Leptophion* species.

***maculipennis* species-group**

This holophyletic group is characterized by the presence of a modified hind tarsal claw; the majority of species have infumate marks in the proximal corner of the marginal cells and in most the genal carina does not join the hypostomal carina. This is the largest species-group and may be subdivided into three apparently holophyletic species-complexes.

***eithos* species-complex.** This group contains four species, *L. eithos* Gauld & Mitchell, *L. ankylosus* Gauld & Mitchell, *L. vernalis* Gauld & Mitchell and *Leptophion* species 1 (BMNH). It is characterized by the highly modified fore wing venation in which $Rs+2r$ is emitted near the centre of the pterostigma. This complex is restricted to Western New Guinea, Sulawesi and the intervening islands.

***radiatus* species-complex.** This group contains six species, *L. radiatus* (Uchida), *L. pterospilus* Gauld & Mitchell, *L. vechii* Gauld & Mitchell, *L. lavellai* Gauld & Mitchell, *L. cheesmanae* Gauld & Mitchell and *L. illustrious* Gauld & Mitchell. It is characterized by the possession of unspecialized hamuli; most species have a rather evenly curved $1m-cu$ and very few have Rs in the hind wing appreciably curved. This group is widely distributed from the Solomon Islands to the Continental Asian mainland.

***maculipennis* species-complex.** This group contains 13 species, *L. maculipennis* (Cameron), *L. pubescens* Gauld & Mitchell, *L. gobius* Gauld & Mitchell, *L. kus* Gauld & Mitchell, *L. justus* Gauld & Mitchell, *L. magus* Gauld & Mitchell, *L. townesi* Gauld & Mitchell, *L. alleni* Gauld & Mitchell, *L. nodus* Gauld & Mitchell, *L. samari* Gauld & Mitchell, *L. samuelsoni* Gauld & Mitchell, *L. quorus* Gauld & Mitchell and *L. longiventris* Cameron. These are the characteristic *Leptophion* species of Cushman (1947) and Townes (1971) in that they possess both a specialized hind tarsal claw and modified penultimate hamulus. Most species have $1m-cu$ very strongly sinuous and Rs in the hind wing strongly bowed. This is the most widespread of all groups with species throughout the Indo-Pacific region. One species has colonized tropical Australia (Gauld, 1984a).

PAMOPHION Gauld

Pamophion Gauld, 1977: 28. Type-species: *Pamophion sorus* Gauld, by original designation.

Mandibles not twisted, weakly narrowed apically, subequally bidentate; outer mandibular surface with subbasal swelling, and with a diagonal groove. Maxillary palp 5-segmented, labial palp 4-segmented; clypeus in profile convex, margin impressed, acute, in anterior aspect weakly convex. Ocelli large, the posterior ones close to the eye margins; frontal carina absent; occipital carina complete except at extreme ventral end. Antennae long and slender. Pronotum unspecialized; spiracular sclerite partially concealed; notauli vestigial; epicnemial carina quite strong, present on mesopleuron; mesopleural furrow undeveloped. Scutellum weakly convex, carinate laterally most of its length; posterior transverse carina of mesosternum incomplete, usually discernible as a discontinuous ridge. Propodeum with anterior area rather short, striate; anterior transcarina complete, other carinae absent, posterior area rugose-reticulate. Fore wing with pterostigma moderately broad; marginal cell long; $Rs+2r$ conspicuously thickened near pterostigma, proximally curved; discosubmarginal cell broadly glabrous anteriorly; $1m-cu$ without a ramellus, moderately sinuous. Hind wing with Rs straight; marginal cell evenly hirsute; hamuli unspecialized. Fore tibial spur without a membranous flange behind the macro-trichial comb; mid and hind trochantelli with a distinct blunt distal tooth; inner hind tibial spur flattened, with a fringe of long, close hairs; hind tarsal claws unspecialized. Gaster slender; tergite 2 in profile very elongate, with thyridia moderately close to anterior margin; umbo absent; epipleuron pendant, narrow. Ovipositor sheath slender, unspecialized.

A single species, *P. sorus*, is known to occur in Queensland. It is apparently the most primitive species in this genus-group. Nothing is known of its biology.

The *ENICOSPILUS* subgroup

This group contains five genera, *Dicamptus*, *Enicospilus*, *Pycnophion*, *Banchogastra* and *Abanchogastra*. The last three are endemic Hawaiian taxa and probably constitute a monophyletic clade which almost certainly arose from within *Enicospilus*. They are so phenetically divergent, however, that it would be quite impractical to include them within *Enicospilus*, an otherwise structurally uniform genus of over 700 species.

The relationship of *Enicospilus* to *Dicamptus* is not clear; the latter may be paraphyletic with respect to the former though subtle differences in venation, alar sclerite form, sculpture and body shape suggest that *Dicamptus* is actually holophyletic.

The *Enicospilus* group is characterized by a number of apomorphic features including having the spiracular sclerite concealed, having an elongate anterior propodeal area, having a rather sinuous $Rs+2r$ and generally having alar sclerites. Individual species may be exceptional in one or two of these features.

Dicamptus, clearly the least specialized genus in this complex, is restricted to the Old World, and *Enicospilus* is apparently most diverse in the Old World tropics, suggesting a palaeotropical origin for the group. Preliminary study of Neotropical species of *Enicospilus* suggests that very few large species-groups occur in South America; several of these also occur in the Nearctic region. The Australian *Dicamptus* and *Enicospilus* have apparently been derived from immigration from South East Asia (Gauld, 1984a).

The Hawaiian genera seem to be a holophyletic group. This is attested by the total lack of alar sclerites, possession of a straight, rather slender $Rs+2r$ and loss of the last 0.3 or so of the lateral scutellar carinae. There are a number of other similarities in sculpture and exact position of wing veins that further supports this clade.

The inter-relationship of these three genera may be misrepresented in the cladogram (Fig. 37). Considering only the characters in the primary data matrix five (16.2, 27.3, 37, 48.1 and 49) support *Pycnophion* + *Abanchogastra* whilst three (13, 42.2, 43.1) support the group *Pycnophion* + *Banchogastra*. None supports the third combination. Of the first five characters 16.2 has almost certainly undergone reversal in *Banchogastra* as the character is apomorphic in the greater part of the presumed ancestral lineage of the species. The plesiomorphic state is otherwise generally only found in primitive ophionines and (again as a reversal) in a few diurnal specialized species (*Banchogastra* has not been taken at light and thus may well be diurnally active). Character 27.3, a centrally interrupted posterior mesosternal carina, is only found in the primary data set in *Pycnophion* and *Abanchogastra*, but this carina is weak centrally in *Banchogastra* and may even be absent narrowly in some specimens. A medioventrally evanescent mesosternal carina can therefore be considered an apomorphy of the Hawaiian genera. Character 49, position of Cu_1 in the fore wing, is plesiomorphic only for *Banchogastra*. The derived condition must therefore be considered to be an apomorphy of the subfamily and the anomalous inclination of this vein in *Banchogastra* is presumably a further specialization, perhaps resulting from the very close proximity of the

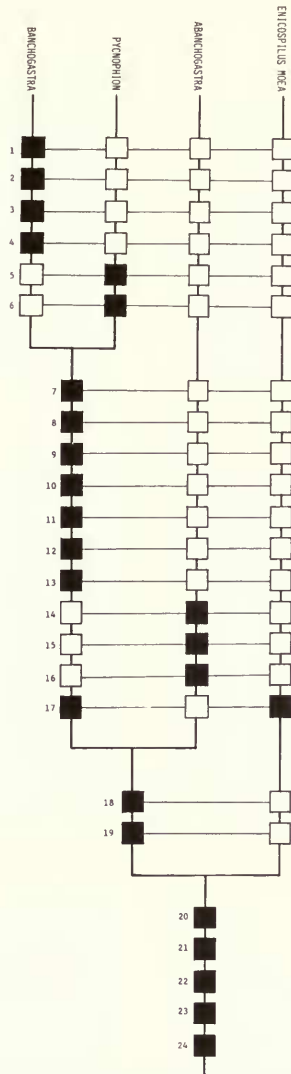


Fig. 37 Putative phylogenetic arrangement of Hawaiian genera in relation to *Enicospilus moea* Cheesman. This cladogram is supported by the following apomorphic features: 1, petiolar spiracles anterior to margin of sternite 1; 2, tergite 2 depressed; 3, epipleuron 2 pendant; 4, further reduction in ocellar size; 5, possession of an elongate ovipositor; 6, loss of hair in discosubmarginal cell centrally; 7, development of a stout gaster; 8, possession of large thyridia close to anterior margin of tergite; 9, metapleuron inflated; 10, epicnemial carina medioventrally incomplete; 11, possession of a short, rounded propodeum; 12, presence of incipient frontal carinae; 13, possession of inflated hind trochanters; 14, loss of occipital carina mediodorsally; 15, upper tooth of mandible compressed; 16, increase in torsion of mandible; 17, reduction in size of ocelli; 18, loss of fenestra; 19, development of fine, granulate thoracic sculpture; 20, loss of alar sclerites; 21, reduction in length of second abscissa of Cu_1 in fore wing; 22, medially evanescent posterior transverse carina of mesosternum; 23, straight and slender $Rs+2r$; 24, loss of posterior part of lateral carina of scutellum.

bases of $1m-cu$ and Cu_{1a} . In some individuals this abscissa of Cu_1 is occluded. The remaining two apomorphies (37 and 48.1) are venational features which are usually rather variable. The three apomorphies uniting *Pycnophion* with *Banchogastra* are slightly more convincing, particularly 42.2, the pterostigma shape. Furthermore, *Pycnophion* and *Banchogastra* resemble each other in many other specialized features. Both have smaller ocelli than normal, have a medioventrally interrupted epicnemial carina, have

a strongly inflated metapleuron and a rather short anterior propodeal area and possess rather inflated trochanters. The thyridia of tergite 2 are large and close to the anterior margin (? a reversal) and the gaster is stouter than most other ophionines. The first segment of the gaster is very much broader and shorter than the corresponding segment in other enicospilines. In view of these marked similarities it would seem that *Pycnophion* + *Banchogastra* constitute a distinct clade.

A Marquesan species, *Enicospilus moea* Cheesman, shares a number of apomorphies with the Hawaiian genera, including possession of a straight, rather slender $Rs+2r$, having a medioventrally obsolescent posterior mesosternal carina and having only the anterior 0.7 of the scutellum carinate. Like the Hawaiian genera the abscissa of Cu_1 between $1m-cu$ and Cu_{1a} is very short and $cu-a$ is well proximal to the base of $Rs&M$. This species does, however, possess fenestra but this, rather than any of the extant Hawaiian species, may be closest to the base of the *Pycnophion/Banchogastra/Abanchogastra* evolutionary line (Fig. 37).

ABANCHOGASTRA Perkins

Abanchogastra Perkins, 1902: 141. Type-species: *Abanchogastra debilis* Perkins, by monotypy.

Mandibles twisted about 45°, strongly and evenly narrowed with teeth subequal, slightly depressed; outer mandibular surface almost flat. Maxillary palp 5-segmented, labial palp 4-segmented; clypeus in profile weakly convex, margin blunt; clypeus in anterior aspect weakly convex. Ocelli large, the posterior ones separated from eye by 0.1–0.2 times their own diameter; frontal carina absent; occipital carina present, mediodorsally interrupted, ventrally weak but joining hypostomal carina. Antennae incomplete. Pronotum unspecialized; spiracular sclerite concealed by pronotal flange; notauli absent; epicnemial carina weak but present on mesopleuron; mesopleural furrow absent. Scutellum weakly convex, carinate laterally about 0.7 of its length; posterior transverse carina of mesosternum centrally obsolescent. Propodeum with anterior area long, striate, carinae absent, posterior area coriaceous. Fore wing with pterostigma of moderate width; marginal cell long; $Rs+2r$ straight and slender; discosubmarginal cell uniformly hirsute; $1m-cu$ evenly curved, without a ramellus. Hind wing with Rs weakly curved. Fore tibial spur without a membranous flange behind macrotrichial comb; mid and hind trochantelli unspecialized; inner hind tibial spur flattened, hind tarsal claws unspecialized. Gaster slender; tergite 2 very elongate, thyridia elliptical, remote from anterior margin, umbo absent; epipleuron up-turned. Ovipositor sheath slender.

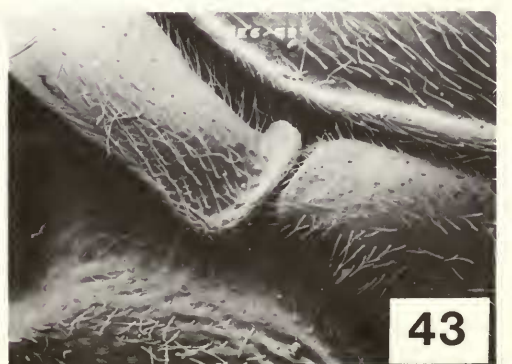
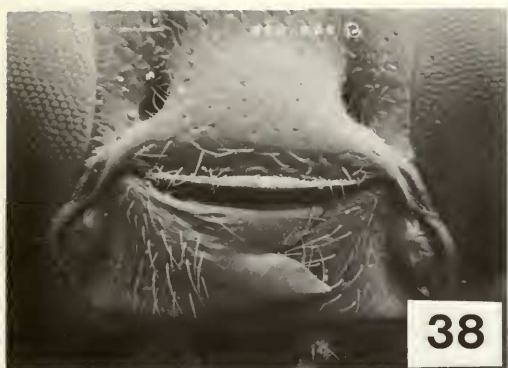
This genus contains a single Hawaiian species which differs strikingly from any *Enicospilus* in the fore wing venation. Nothing is known of its biology.

BANCHOGASTRA Ashmead

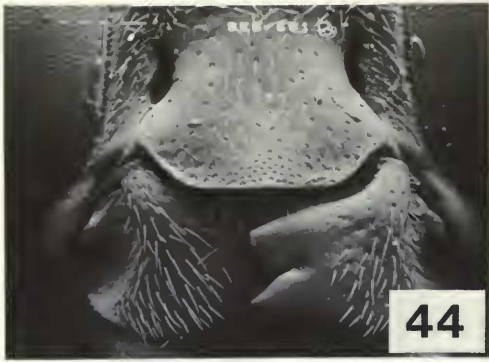
Banchogastra Ashmead, 1900: 87. Type-species: *Banchogastra nigra* Ashmead, by original designation.

Mandibles twisted about 25°, strongly and evenly narrowed apically with upper tooth a little longer than the lower; outer mandibular surface with strong proximal concavity, remainder of surface virtually flat but with diagonal tract of dense hair. Maxillary palp 5-segmented, labial palp 4-segmented; clypeus in profile weakly convex, margin sharp, not impressed at all; clypeus in anterior aspect with margin very weakly convex. Ocelli small, the posterior ones separated from eyes by more than their own minimum diameter; frontal carina very weak but discernible; occipital carina complete, ventrally not quite reaching hypostomal carina. Antennae moderately slender, about 1.2 times length of fore wing. Pronotum unspecialized; spiracular sclerite completely occluded by pronotal flange; notauli weak; epicnemial carina strong, present on mesopleuron but medioventrally interrupted; mesopleural groove virtually absent. Scutellum convex, carinate laterally about 0.8 of its length; posterior transverse carina of mesosternum complete, or slightly weak medioventrally. Propodeum with anterior area moderately short but clearly discernible; anterior transverse carina complete; posterior transverse carina vestigial, others absent; posterior area rugose. Fore wing with pterostigma moderately slender; marginal cell long; discosubmarginal cell evenly hirsute; $Rs+2r$ straight, expanded slightly immediately before joining pterostigma; $1m-cu$ evenly arcuate, ramellus absent; unusual in having $1m-cu$ and Cu_{1a} basally contiguous or united. Hind wing with Rs almost straight. Fore tibial spur without a membranous flange behind macrotrichial comb; mid and hind trochantelli short and stout, otherwise unspecialized; inner hind tibial spur slightly flattened, with a fringe of fine hairs; hind tarsal claws long but closely pectinate. Gaster stout; tergite 2 depressed, barely longer than deep, not longer than broad; thyridia large, oval, close to anterior margin; umbo absent; laterotergite narrow, pendant. Ovipositor sheath short, slender.

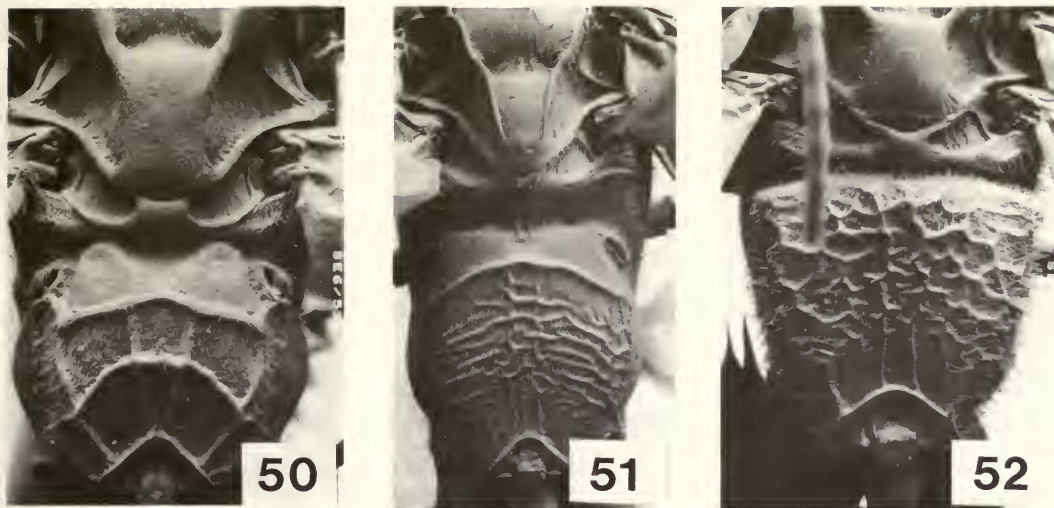
Banchogastra is a small genus containing two Hawaiian species (Townes, 1971). Nothing is known of their biology.



Figs 38–43 Stereoscan photographs of ophionines: 38–41, mandibles of (38) *Ophion* sp.; (39) *Ophiogastrella* sp.; (40) *Enicospilus* sp.; (41) *Leptophion alleni* Gauld & Mitchell. 42, 43, hind corner of pronotum and spiracular sclerite of (42) *Ophion* sp.; (43) *Enicospilus* sp.



Figs 44–49 Stereoscan photographs of Ophioninae: 44, mandibles of *Thyreodon* sp. 45–47, hind tarsal claws of (45) *Ophion* sp. ♀; (46) *Leptophion* sp. ♀; (47) *Ophiogastrella* sp. ♂. 48, 49, fore tibial spurs of (48) *Ophion* sp.; (49) *Enicospilus* sp.



Figs 50–52 Stereoscan photographs of dorsal region of posterior part of alitrunk of: 50, *Ophion* sp.; 51, *Enicospilus* sp.; 52, *Thyreodon* sp.

DICAMPTUS Szépligeti

Dicamptus Szépligeti, 1905: 21. Type-species: *Dicamptus giganteus* Szépligeti, by monotypy.

Mandibles not twisted, generally very weakly narrowed, almost equally bidentate; outer mandibular surface weakly convex with proximal concavity, sometimes with pronounced proximal swelling and diagonal hirsute groove. Maxillary palp 5-segmented, labial palp 4-segmented; clypeus in profile from flat to convex or even pyramidal, usually with margin impressed and acute; clypeus in anterior aspect truncate or weakly convex. Ocelli generally large, the posterior ones usually virtually contiguous with eyes except in a few Afrotropical species; frontal carina absent; occipital carina usually complete, ventrally joining hypostomal carina. Antennae moderately to extremely elongate, from slightly longer than fore wing to 2.0 times fore wing length and with upwards of 90 flagellar segments. Pronotum unspecialized; spiracular sclerite virtually completely concealed by pronotal lobe; notauli vestigial or absent; epicnemial carina usually complete, often strong; mesopleural furrow generally absent. Scutellum weakly to moderately convex, with lateral longitudinal carinae strong, usually complete; posterior transverse carina of mesosternum complete. Propodeum with anterior area long, striate; anterior transverse carina usually complete and other carinae obsolescent or absent; posterior area usually coarsely reticulate. Fore wing with pterostigma fairly slender; marginal cell very long; $Rs+2r$ broadened and variously sinuate before joining pterostigma; discosubmarginal cell with a large glabrous fenestra near anterior corner, this fenestra bearing at least one sclerite (proximal one); $1m-cu$ from arcuate to sinuous, usually without a ramellus. Hind wing with Rs virtually straight. Fore tibial spur without a membranous flange behind macrotrichial comb; mid and hind trochantelli unspecialized; inner hind tibial spur flattened, with a margin of long close hairs; hind tarsal claws unspecialized. Gaster slender; tergite 2 very elongate, with thyridia remote from anterior margin; umbo absent; epipleuron up-turned. Ovipositor sheath slender.

Dicamptus is a moderate-sized genus with 27 described species and two undescribed species (ANIC; BMNH) in the Palaeotropical region. A few species extend into temperate areas, *D. fuscicornis* (Erichson) reaches Tasmania and *D. nigropictus* (Matsumura) occurs northwards as far as Japan and Korea.

Two quite distinct species-groups are recognizable. The *pulchellus* group comprises gracile species with a very small cubital index (0.55 or less), a short vein $3r-m$ (less than 0.5 of the length of M between $2m-cu$ and $3r-m$) and a fairly well-developed mandibular groove. This group contains *D. collessi* Gauld, *D. uptoni* Gauld and *Dicamptus* species 1 (ANIC) which are Australian endemics, *D. indicus* Nikam and *D. fuscicornis* which are widespread Indo-Australian species, *D. ishikii*, an Oriental species and the Afrotropical species *D. crassellus* (Morley), *D. xhosa* Delobel, *D. betsileo* Delobel, *D. pellucidus* (Kriechbaumer), *D. seyrigi* Delobel, *D. townesi* Delobel and *D. pulchellus* (Morley).

The remaining species (the *giganteus* group) are in general very much larger insects with a larger cubital index, a longer $3r-m$ and stouter mandibles. This may well be a paraphyletic grade-group, as almost

certainly the characters defining it are plesiomorphic for the genus. The majority of species in this group occur in areas with a pronounced dry season, particularly parts of Africa and India. Some of the very largest species (*reticulatus* (Cameron), *nigropictus* (Matsumura) and *giganteus* Szépligeti) occur in montane forest, a very wet habitat. None of the species in the *giganteus* group occur east of Weber's line. In New Guinea they seem to have been replaced by some exceptionally large species of *Enicospilus* (*E. enormous* Gauld & Mitchell species complex).

ENICOSPILUS Stephens

- Enicospilus* Stephens, 1835: 126. Type-species: *Ophion merdarius* Gravenhorst sensu Stephens (= *Ichneumon ramidulus* L.), by subsequent monotypy, Stephens, 1845.
- Henicospilus* Agassiz, 1846: 138. [Unjustified emendation.]
- Allocampytus* Foerster, 1869: 150. Type-species: *Ophion undulatus* Gravenhorst, by subsequent designation, Thömsen, 1888: 1189.
- Dispilus* Kriechbaumer, 1894b: 309. Type-species: *Ophion (Dispilus) natalensis* Kriechbaumer, by monotypy.
- Pleuroneurophion* Ashmead, 1900: 86. Type-species: *Pleuroneurophion hawaiiensis* Ashmead, by original designation.
- Cymatoneura* Kriechbaumer, 1901a: 22. Type-species: *Ophion undulatus* Gravenhorst, by subsequent designation, Viereck, 1914: 8.
- Pterospilus* Kriechbaumer, 1901c: 156. Type-species: *Ophion (Enicospilus) dubius* Tosquinet, by subsequent designation, Viereck, 1914: 126. [Junior homonym of *Pterospilus* Rondani, 1856.]
- Trispilus* Kriechbaumer, 1901c: 156. Type-species: *Ophion (Enicospilus) trimaculatus* Tosquinet (= *Henicospilus seminiger* Szépligeti), by monotypy.
- Metophion* Szépligeti, 1905: 28. Type-species: *Metophion bicolor* Szépligeti, by subsequent designation, Viereck, 1914: 94.
- Ceratospilus* Szépligeti, 1905: 28. Type-species: *Ceratospilus biroi* Szépligeti, by monotypy.
- Atoponeura* Szépligeti, 1905: 34. Type-species: *Atoponeura concolor* Szépligeti (= *Enicospilus atoponeurus* Cushman), by monotypy.
- Ophiomorpha* Szépligeti, 1905: 34. Type-species: *Ophion curvinervis* Cameron (= *Enicospilus cameronii* Dalla Torre), by subsequent designation, Hooker, 1912: 134. [Junior homonym of *Ophiomorpha* Nilsson, 1836.]
- Cryptocampytus* Brèthes, 1909: 230. [Unnecessary replacement name for *Allocampytus* Foerster.]
- Eremotyloides* Perkins, 1915: 530. Type-species: *Eremotyloides orbitalis* Ashmead, by monotypy.
- Amesospilus* Enderlein, 1918: 222. Type-species: *Ophion unicallosus* Snellen, by original designation.
- Schizospilus* Seyrig, 1935: 79. Type-species: *Schizospilus divisus* Seyrig, by original designation.

Mandibles twisted from 10 to 90°, weakly to very strongly narrowed, from equally bidentate to with upper tooth conspicuously the longer, rarely with lower tooth the longer; outer mandibular surface usually with a proximal concavity, the remainder either almost flat or with a diagonal hirsute groove. Maxillary palp 5-segmented, labial palp 4-segmented; clypeus in profile from flat to nasute, with margin blunt or acute or acute and subapically impressed; clypeus in anterior aspect usually weakly convex, rarely truncate or concave, in one Neotropical species with an indication of a median tooth. Ocelli usually large, generally with the posterior ones very close to or contiguous with the eyes, in a few species with the ocelli smaller; frontal carina absent; occipital carina usually complete, sometimes mediodorsally obsolescent or interrupted. Antennae usually more than 1.5 times as long as the fore wing. Pronotum usually unspecialized, in some Madagascan species with median transverse crests; spiracular sclerite almost always completely occluded by flange of pronotum; notauli vestigial or absent; epicnemial carina usually well developed, present on mesopleuron, usually reaching to level of lower corner of pronotum; mesopleural furrow usually absent. Scutellum from almost flat to strongly convex, almost always with strong lateral carinae virtually entire, rarely with these carinae short; posterior transverse carina of mesosternum usually complete. Propodeum with anterior area moderately long to long, generally striate; anterior transverse carina of propodeum usually present, almost always complete; posterior transverse carina usually absent, rarely present laterally; posterior area usually reticulate or rugose, sometimes finely irregularly wrinkled, in a few species concentrically striate, very rarely the posterior area almost smooth or punctate. Fore wing with pterostigma moderately broad to quite slender; marginal cell long; $Rs+2r$ almost always broadened and variously sinuate before joining the pterostigma; discosubmarginal cell usually with a glabrous fenestra adjacent to the vein $Rs+2r$, this fenestra often bearing one or more detached sclerites; $1m-cu$ usually arcuate or sinuous, rarely somewhat angulate; ramellus usually absent, rarely in one or two species well-developed. Hind wing with Rs straight or weakly bowed. Fore tibial spur without a membranous

flange behind macrotrichial comb; mid and hind trochantelli usually simple, rarely with a marginal tooth; inner hind tibial spur flattened, with margin of close long hairs; hind tarsal claws various, most usually unspecialized and slightly sexually dimorphic, sometimes extremely sexually dimorphic, the male having a very fine pectinal comb, in a few taxa with the claws strongly geniculate, occasionally with the claws asymmetrical, in other taxa with the distal pectina projecting beyond the apex of the true claw, and very rarely, in a few eremic species, with the pectina reduced. Gaster from moderately stout to very slender; tergite 2 usually very long and slender, rarely posteriorly almost as deep as long, almost always with thyridia remote from anterior margin; umbo vestigial or absent; epipleuron usually up-turned, pendant in a few (or one) Neotropical species. Ovipositor sheath slender; ovipositor usually short, straight, in isolated taxa it may be upcurved or decurved, and very rarely it may be straight but project well beyond the apex of the gaster.

Enicospilus is an extremely large genus, most species of which occur in the tropics. The major centres of radiation appear to be New Guinea, where there are about 200 endemic species, and Madagascar, which has about half that number. The Philippines, Hawaii and Zaire river basin are other areas of pronounced endemicity. In the tropics, the greatest diversity of species seems to occur at mid-elevation in the cloud forests (moss forests) between 1200 and 2000 m. A number of species are restricted to areas that have a pronounced dry season (e.g. *Enicospilus capensis*), and a few species seem to inhabit deserts (e.g. *E. psammus*). Many species are capable of sustained flight over great distances (e.g. across the Tasman Sea from Australia to New Zealand) and several occur on almost all South Pacific archipelagos as far east as the Tuamotus. Most small oceanic islands apparently have several species of *Enicospilus* present, and on the Micronesian islands six of the 33 recorded ichneumonids are *Enicospilus* (Townes, 1958). Outside the tropics there are notably fewer species. Scaramozzino (1983) records only ten from Italy whilst Viktorov (1957) knew of only 15 species from the Soviet Union. Five nominal species are recorded from Britain, but probably only four species occur there (Fitton *et al.*, 1978).

Certain generalized distribution patterns can be observed in the genus. New Guinea and Madagascar have large numbers of endemic species in endemic species-groups; for example eight of the 24 species-groups recognized as occurring in the Afrotropical region are restricted to Madagascar, and these eight groups contain 35 species (Gauld & Mitchell, 1978). The Philippines, Hawaii and South America each contain very few species-groups, but these may be very large. Relatively few of the numerous other species-groups are endemic to a single zoogeographic area. Several of the species-groups that are widespread in South East Asia have their greatest diversity in New Guinea (e.g. the *xanthocephalus* and *tremulus* species-groups, Gauld & Mitchell, 1981). Virtually no widespread South East Asian groups have a localized centre of diversity outside Melanesia; most species seem to be widespread with isolated local endemics (e.g. the *flavicaput* species-group, Gauld & Mitchell, 1981). Many widespread South East Asian groups are also represented in mainland Africa (e.g. the *capensis* and *antefurcalis* species-groups). A number of species-groups are either endemic to mainland Africa (e.g. the *babaultii*, *biimpressus* and *rubens* species-groups) or are most diverse in Africa (e.g. the *dolosus* species-group). Most species occurring in the Palaearctic region belong to species-groups that are well-represented in the Nearctic region, but neither region appears to have any endemic species-groups, nor is any species-group endemic to the Holarctic region. The *Enicospilus* species of Australia are virtually all either widespread South East Asian species or are endemics derived from South East Asia (Gauld, 1984a). New Zealand has no endemic species, but shares two with Australia. A distinct faunal region is apparent which comprises part of the Mediterranean basin, most of the Middle East and extends eastwards into Central Asia and south-eastwards into north-west India. Although the fauna of this area is poorly known, it seems that at least one species-group may be endemic to the region (the *przewalskii* species-group).

Gauld & Mitchell (1978; 1981) outline a very large number of species-groups and several of these are refined by Gauld (1984a). Large numbers of other species are currently unplaced; these may belong to less clearly definable groups, or they may be aberrant members of existing groups, or they may represent numerous monobasic species-groups. The phylogenetic inter-relationships of most of these species-groups are very difficult to assess as most are definable on the basis of a number of autapomorphies. Few share obvious specializations with other species-groups.

Repeated attempts have been made to subdivide *Enicospilus* into a number of smaller genera (Kriechbaumer, 1901c; Szépligeti, 1905; Seyrig, 1935) but none of these subdivisions has endured, largely for two reasons – the authors proposing the separation have very limited experience of the range of morphological diversity afforded by the genus, and the characters used to effect separation are superficial differences, usually in the number of alar sclerites. The clearest demonstration of the great variability of alar sclerite form and number can be seen between the closely related species of the *unidens* species-group, a group definable by several autapomorphies. The proximal sclerite is present in all species but only *E. unidens* has a central sclerite; the distal sclerite is present in *E. unidens*, *E. akainus* and *E. mirax* but absent

in *E. gonidius* and *E. amygdalis*. The most important features for recognizing apparently 'natural' groupings seem to be the form of the tarsal claws (including the degree of sexual dimorphism), the structure of the mandibles and clypeus, the presence or absence of the proximal sclerite and the structure of the male genitalia.

Little is known of the biology of species of *Enicospilus*. The majority of host records refer to species parasitizing larvae of Noctuidae, Geometridae, Lymantriidae or Saturniidae. A few species attack pyralids. Many of the larger species that attack saturniid larvae spin their cocoon within the host cocoon, but other species spin a cocoon that is not enclosed by that of the host. Most species seem to attack larvae that are free-living, tree-leaf-feeding caterpillars, but the few with longer ovipositors seem to attack larvae mining stems (e.g. *E. terebrus*). It must be stressed that the hosts of the majority of tropical species are not known.

PYCNOPHION Ashmead

Pycnophion Ashmead, 1900: 87. Type-species: *Pycnophion molokaiensis* Ashmead, by monotypy.

Mandibles twisted about 20°, evenly tapered, with upper tooth broader but of about equal length to the lower tooth; outer mandibular surface slightly concave, sparsely pubescent. Maxillary palp 5-segmented, labial palp 4-segmented; clypeus in profile moderately convex, margin blunt; clypeus in anterior aspect weakly convex. Ocelli moderately large, the posterior ones separated from the eye by about 0.5 times their own diameter; frontal carina very weak; occipital carina complete, mediodorsally with a depression. Antennae moderately long, about 1.3 times the length of the fore wing. Pronotum slightly flattened mediodorsally; spiracular sclerite covered by pronotal flange; notauli vestigial; epicnemial carina strong, curved to nearly reach the anterior margin of the pleuron above the level of the lower corner of the pronotum; mesopleural furrow absent. Scutellum convex, laterally carinate at least 0.6 of its length; posterior transverse carina of the mesosternum centrally obsolescent. Propodeum with anterior area moderately short but clearly discernible; anterior transverse carina complete, at least centrally, the posterior one vestigial, the other absent; posterior area finely coriaceous. Pterostigma moderately slender; marginal cell long; *Rs+2r* virtually straight, evenly but abruptly widened before joining pterostigma; discosubmarginal cell with an ill-defined glabrous area anteriorly, the entire cell very sparsely hirsute; *1m-cu* fairly evenly arcuate, ramellus absent. Hind wing with *Rs* straight. Fore tibial spur without a membranous flange behind macrotrichial comb; mid and hind trochantelli unspecialized; inner hind tibial spur somewhat flattened, with a fringe of long hairs; tarsal claws unspecialized. Gaster moderately stout; tergite 2 in profile, slightly longer than posteriorly deep, with thyridia large, oval and close to anterior margin; umbo vestigial; epipleuron up-turned. Ovipositor exceptional in being very long and up-curved, reaching beyond apex of gaster by at least length of tergites 2–5.

Pycnophion is a small genus containing three Hawaiian species (Townes *et al.*, 1961). It is one of the most atypical of ophonine genera and females superficially resemble campoplegines or phygadeuontines. One species, *P. fuscipennis* Perkins, has been reared as a parasite of the larvae of *Hyposmocoma chilonella* (Lepidoptera: Cosmopterygidae) (Swezey, 1931) which are borers in the pith of stems of *Rubus*, *Acacia* and a variety of other woody plants.

Acknowledgements

Much of this work was undertaken as part of a PhD thesis under the supervision of Dr Garth Underwood. I am extremely grateful for his advice at all stages of the study. I would like to thank Dr J. Felsenstein for providing a copy of his program PHYLIP, and the staff of the computing centre at the City of London Polytechnic for their assistance with computational problems. I am grateful to many of my colleagues at the British Museum (Natural History) for their opinions on various problems and comments on various drafts, though the conclusions expressed do not necessarily reflect their points of view; in particular I would like to thank Dr A. D. Austin, Mr B. Bolton, Mr M. C. Day, Dr M. G. Fitton, Dr J. D. Holloway, Dr L. A. Mound, Dr G. S. Robinson, Mr R. I. Vane-Wright and Dr P. Whalley. I am grateful to the following for lending me particularly interesting specimens from the collections in their care: Dr D. Kasparayan, Dr H. Townes and Dr L. Zombori, and I am particularly grateful to all those entomologists, too numerous to mention, who have sent me ophonines from all over the world. Finally I would like to thank Mr J. Carter for taking the stereoscan pictures and Ms P. A. Mitchell for typing the manuscript.

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Appendix 1 The opionine taxa used in the cladistic study.

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|-----|--|-----------------------------|
| 901 | <i>Thyreodon atricolor</i> (Olivier) | Nearctic |
| 902 | <i>Thyreodon laticinctus</i> Cresson | Neotropical |
| 903 | <i>Thyreodon fulvescens</i> Cresson | Neotropical |
| 904 | <i>Thyreodon flamminiger</i> (Morley) | Neotropical |
| 905 | <i>Simophion calvus</i> Viktorov | Palaeartic |
| 906 | <i>Orientospilus melasma</i> Townes | Afrotropical |
| 907 | <i>Dictyonotus purpurascens</i> (Smith) | Oriental/Eastern Palaeartic |
| 908 | <i>Rhynchophion flammipennis</i> (Ashmead) | Neotropical |
| 909 | <i>Lepiscelus distans</i> (Seyrig) | Afrotropical |
| 910 | <i>Ophiogastrella</i> sp. 1 (BMNH) | Neotropical |
| 911 | <i>Ophiogastrella</i> sp. 2 (BMNH) | Neotropical |
| 912 | <i>Laticoleus unicolor</i> (Szépligeti) | Afrotropical |
| 913 | <i>Laticoleus pronotalis</i> Gauld & Mitchell | Afrotropical (Madagascar) |
| 914 | <i>Laticoleus spilus</i> Gauld & Mitchell | Afrotropical |
| 915 | <i>Laticoleus curvatus</i> Delobel | Afrotropical |
| 916 | <i>Stauropoctonus bombycivorus</i> (Gravenhorst) | Palaeartic |
| 917 | <i>Stauropoctonus occipitalis</i> Gauld & Mitchell | Afrotropical (Madagascar) |
| 918 | <i>Aulophion</i> sp. 1 (BMNH) | Neotropical |
| 919 | <i>Pamophion sorus</i> Gauld | Australian |
| 920 | <i>Riekophion emandibulator</i> (Morley) | Australian |
| 921 | <i>Ophionopsis nigrocyaneus</i> Tosquinet | Afrotropical |
| 922 | <i>Sicophion pleuralis</i> Gauld | Neotropical |
| 923 | <i>Prethophion latus</i> Townes | Neotropical |
| 924 | <i>Pycnophion molokaiensis</i> Ashmead | Hawaiian |
| 925 | <i>Abanchogastra hawaiiensis</i> (Ashmead) | Hawaiian |
| 926 | <i>Banchogastra nigra</i> Ashmead | Hawaiian |
| 927 | <i>Barytatocephalus mocsaryi</i> (Brauns) | Palaeartic |
| 928 | <i>Leptophion maculipennis</i> (Cameron) | Oriental |
| 929 | <i>Leptophion anici</i> Gauld | Australian/New Caledonian |
| 930 | <i>Leptophion pterospilus</i> Gauld & Mitchell | Oriental |
| 931 | <i>Leptophion tetus</i> Gauld | Australian |
| 932 | <i>Dicamptus neavei</i> Gauld & Mitchell | Afrotropical |
| 933 | <i>Dicamptus giganteus</i> Szépligeti | Oriental |
| 934 | <i>Dicamptus fuscicornis</i> (Erichson) | Oriental/Australian |
| 935 | <i>Euryophion latipennis</i> (Kirby) | Afrotropical |
| 936 | <i>Euryophion adustus</i> (Townes) | Afrotropical |
| 937 | <i>Rictophion ikuthana</i> (Kriechbaumer) | Afrotropical |
| 938 | <i>Xylophion xylus</i> (Gauld) | Australian/Papuan |
| 939 | <i>Ophion luteus</i> (L.) | Palaeartic |
| 940 | <i>Eremotylus boguschi</i> (Meyer) | Palaeartic |
| 941 | <i>Agathophiona fulvicornis</i> Westwood | Neotropical |
| 942 | <i>Enicospilus tremulus</i> Gauld & Mitchell | Oriental |
| 943 | <i>Enicospilus spathius</i> Gauld & Mitchell | Oriental |
| 944 | <i>Enicospilus nephele</i> Gauld & Mitchell | Oriental |
| 945 | <i>Enicospilus cionobius</i> Gauld & Mitchell | Oriental |
| 946 | <i>Enicospilus unidens</i> Seyrig | Afrotropical |
| 947 | <i>Enicospilus mahaloniensis</i> Gauld & Mitchell | Afrotropical (Madagascar) |
| 948 | <i>Rhopalophion discinervis</i> (Morley) | Afrotropical |
| 949 | <i>Janzophion nebosus</i> sp. n. | Neotropical |
| 950 | <i>Hellwigiella nigripennis</i> Szépligeti | Palaeartic |
| 951 | <i>Sclerophion uchidai</i> Gauld & Mitchell | Oriental/Eastern Palaeartic |

Hypothetical taxa

| | | | |
|-----|--------------------------------|-----|---------------------------------------|
| 960 | <i>Laticoleus</i> ancestor | 964 | <i>Thyreodon/Dictyonotus</i> ancestor |
| 961 | <i>Ophiogastrella</i> ancestor | 965 | <i>Euryophion</i> ancestor |
| 962 | <i>Leptophion</i> ancestor | 966 | <i>Dicamptus</i> ancestor |
| 963 | <i>Stauropoctonus</i> ancestor | 967 | <i>Enicospilus</i> ancestor |

Appendix 2 Primary data matrix of 51 selected ophionines and 95 characters. 0 indicates a presumed plesiomorphic condition, 1 a presumed apomorphic state.

| | 1.1 | 2 | 4.1 | 5.1 | 6.1 | 7.1 | 8.1 | 9 | 11 | 13 | 14.2 | 15.2 | | | | | | | | |
|-----|-----|---|-----|-----|-----|-----|-----|----|----|------|------|------|---|---|---|---|---|---|---|---|
| | 1.2 | 3 | 4.2 | 5.2 | 6.2 | 7.2 | 8.2 | 10 | 12 | 14.1 | 15.1 | 16.1 | | | | | | | | |
| 901 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 902 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 |
| 903 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| 904 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 |
| 905 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| 906 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 |
| 907 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 |
| 908 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 |
| 909 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 |
| 910 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| 911 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| 912 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 |
| 913 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 |
| 914 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 |
| 915 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 |
| 916 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 |
| 917 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 |
| 918 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 |
| 919 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 |
| 920 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| 921 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 |
| 922 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 1 |
| 923 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 |
| 924 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 |
| 925 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 |
| 926 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 1 |
| 927 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 |
| 928 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 |
| 929 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 |
| 930 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 |
| 931 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 |
| 932 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 1 |
| 933 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 |
| 934 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 |
| 935 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| 936 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 |
| 937 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| 938 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| 939 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| 940 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| 941 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 1 |
| 942 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 |
| 943 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 |
| 944 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 |
| 945 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 |
| 946 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 |
| 947 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 |
| 948 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 |
| 949 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 |
| 950 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 |
| 951 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 |

Appendix 2 – cont.

| | 16.2 | 18.1 | 19 | 20.2 | 21.2 | 22.2 | 24.1 | 25.1 | 26 | 27.2 | 28.1 | 29.1 | | | | | | | | | | | | | |
|-----|------|------|------|------|------|------|------|------|------|------|------|------|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 17 | 18.2 | 20.1 | 21.1 | 22.1 | 23 | 24.2 | 25.2 | 27.1 | 27.3 | 28.2 | 29.2 | | | | | | | | | | | | | |
| 901 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 1 |
| 902 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 1 |
| 903 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 1 |
| 904 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 |
| 905 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 |
| 906 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 0 |
| 907 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 |
| 908 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | |
| 909 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 |
| 910 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | |
| 911 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | |
| 912 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | |
| 913 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | |
| 914 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | |
| 915 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | |
| 916 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 |
| 917 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 |
| 918 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | |
| 919 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 |
| 920 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | |
| 921 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 |
| 922 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 0 |
| 923 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 |
| 924 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 |
| 925 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 |
| 926 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 |
| 927 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 |
| 928 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 |
| 929 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 0 |
| 930 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 |
| 931 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 |
| 932 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 |
| 933 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 |
| 934 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 |
| 935 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 |
| 936 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 |
| 937 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 0 |
| 938 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 |
| 939 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| 940 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| 941 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 |
| 942 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 |
| 943 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 |
| 944 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 |
| 945 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 |
| 946 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 |
| 947 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 |
| 948 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 |
| 949 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 |
| 950 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 |
| 951 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 |

Appendix 2 - cont.

| | 30 | 32 | | 34 | 36.1 | | 36.3 | 38 | 40 | 42.1 | 43.1 | 44.1 | 45.1 | 46 | 47.2 | | |
|-----|----|----|----|------|------|----|------|------|------|------|------|------|------|----|------|---|---|
| | 31 | 33 | 35 | 36.2 | 37 | 39 | 41 | 42.2 | 43.2 | 44.2 | 45.2 | 47.1 | | | | | |
| 901 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 |
| 902 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| 903 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 |
| 904 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 |
| 905 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 |
| 906 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 |
| 907 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 |
| 908 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 |
| 909 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 0 |
| 910 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 |
| 911 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 |
| 912 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 1 |
| 913 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 |
| 914 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 |
| 915 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 |
| 916 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 |
| 917 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 |
| 918 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 0 |
| 919 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 1 |
| 920 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 1 |
| 921 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 |
| 922 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| 923 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 |
| 924 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 |
| 925 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 |
| 926 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 |
| 927 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 |
| 928 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 0 |
| 929 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 1 |
| 930 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 |
| 931 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 |
| 932 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 1 |
| 933 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 1 |
| 934 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 1 |
| 935 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 |
| 936 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 0 |
| 937 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 |
| 938 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 |
| 939 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 |
| 940 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 |
| 941 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| 942 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 1 |
| 943 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 1 |
| 944 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 0 |
| 945 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 1 |
| 946 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 1 |
| 947 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 1 |
| 948 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| 949 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 1 |
| 950 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 |
| 951 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 0 |

Appendix 2 - cont.

| | 48.1 | 49 | 51.1 | 52.1 | 53 | 55 | 57 | 58.2 | 60 | 61.2 | 63 | | | | | | | | | | | |
|-----|------|----|------|------|----|----|------|------|------|------|----|---|---|---|---|---|---|---|---|---|---|---|
| | 48.2 | 50 | 51.2 | 52.2 | 54 | 56 | 58.1 | 59 | 61.1 | 62 | 64 | | | | | | | | | | | |
| 901 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | | |
| 902 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| 903 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 |
| 904 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| 905 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 |
| 906 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 |
| 907 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| 908 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| 909 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 |
| 910 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 |
| 911 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 1 |
| 912 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 |
| 913 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 |
| 914 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 |
| 915 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 |
| 916 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 0 |
| 917 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 |
| 918 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 |
| 919 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 |
| 920 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| 921 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 922 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 |
| 923 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 |
| 924 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 |
| 925 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 |
| 926 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 |
| 927 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| 928 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 |
| 929 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 |
| 930 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 |
| 931 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 |
| 932 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 |
| 933 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 |
| 934 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 |
| 935 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 |
| 936 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 |
| 937 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 |
| 938 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 |
| 939 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 940 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 |
| 941 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 942 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 0 |
| 943 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 |
| 944 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 |
| 945 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 |
| 946 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 |
| 947 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 |
| 948 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| 949 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 |
| 950 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| 951 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 |

Appendix 4 Primary labels matrix derived from analysis of 51 selected ophionines. The figure in brackets to the immediate right of the taxon number indicates the number of times that taxon alone is responsible for the failure of a character in the LeQuesne test. Notably high values in any column suggest that a particular character state shared by the respective characters is likely to be the result of parallel development or reversal. For example, character 1-2 has high values for taxa 909 and 923; as both taxa share an apomorphic 1 state, the labels matrix suggests this condition has been independently derived in the two taxa, and thus should not be considered a synapomorphy uniting 909 + 923.

| | 1.1 | 2 | 4.1 | 5.1 | 6.1 | 7.1 | 8.1 | 10 | 13 | 14.2 | 15.2 | 16.2 | | | | | | | | |
|----------|-----|----|-----|-----|-----|-----|-----|----|------|------|------|------|----|----|----|----|----|----|----|----|
| | 1.2 | 3 | 4.2 | 5.2 | 6.2 | 7.2 | 9 | 12 | 14.1 | 15.1 | 16.1 | | | | | | | | | |
| 901 (5) | -- | -- | -- | -- | -- | -- | -- | 1 | -- | -- | -- | -2 | | | | | | | | |
| 902 (7) | -- | -- | 1 | -- | -- | -- | 1 | -- | -- | 1 | -- | 2 | | | | | | | | |
| 903 (11) | -- | -- | -- | -- | -- | 1 | -- | 1 | 1 | 1 | -- | 5 | | | | | | | | |
| 904 (6) | -- | -- | 1 | -- | -- | -- | 2 | -- | -- | -- | -- | -- | | | | | | | | |
| 905 (10) | -- | -- | -- | -- | -- | 2 | -- | -- | -- | 1 | -- | -- | | | | | | | | |
| 906 (48) | -- | -- | -- | 11 | -- | -- | 5 | -- | -- | 6 | -- | -- | | | | | | | | |
| 907 (12) | -- | -- | -- | -- | -- | 1 | -- | 1 | -- | -- | -- | 1 | | | | | | | | |
| 908 (67) | 1 | -- | 3 | -- | 22 | 2 | -- | 5 | 1 | -- | 34 | 3 | -- | 2 | 1 | 2 | 2 | -- | -- | |
| 909 (89) | 3 | 11 | -- | 2 | 13 | -- | -- | 7 | -- | 2 | -- | -- | 1 | -- | -- | 3 | 1 | -- | -- | 6 |
| 910 (6) | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | 1 |
| 911 (6) | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | 2 |
| 914 (6) | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | 1 | -- | -- | -- | -- |
| 915 (34) | 1 | 1 | -- | 2 | 1 | -- | -- | 1 | -- | 1 | -- | -- | -- | -- | -- | 1 | -- | -- | -- | 1 |
| 916 (5) | -- | 1 | -- | -- | -- | -- | 1 | -- | -- | -- | -- | -- | -- | -- | 1 | -- | -- | -- | -- | -- |
| 917 (13) | -- | -- | -- | -- | -- | 3 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- |
| 918 (19) | -- | 2 | -- | -- | -- | 4 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- |
| 919 (2) | -- | -- | -- | 1 | -- | -- | -- | -- | 1 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- |
| 920 (9) | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | 1 | -- | -- | -- | -- |
| 921 (56) | -- | -- | 2 | -- | -- | -- | -- | 3 | 2 | -- | -- | 5 | -- | 1 | 3 | 2 | -- | -- | -- | 12 |
| 922 (85) | 4 | -- | 1 | -- | 12 | 6 | -- | 1 | 1 | 2 | -- | -- | 34 | 1 | -- | 1 | 5 | 2 | 11 | -- |
| 923 (45) | 5 | 13 | 1 | -- | -- | -- | -- | -- | 1 | -- | -- | 14 | -- | -- | 1 | 1 | -- | -- | -- | -- |
| 924 (13) | 1 | -- | -- | -- | -- | 1 | -- | -- | -- | -- | -- | -- | -- | 2 | -- | -- | -- | -- | -- | -- |
| 925 (30) | 4 | -- | -- | -- | 1 | 7 | -- | -- | -- | -- | -- | -- | -- | 1 | -- | 1 | -- | 1 | -- | -- |
| 926 (14) | -- | -- | -- | -- | 3 | -- | -- | -- | -- | -- | -- | -- | 2 | 2 | -- | -- | -- | 1 | -- | -- |
| 927 (42) | 1 | 1 | -- | 10 | 1 | -- | -- | 1 | -- | 3 | -- | -- | 1 | -- | -- | 1 | 1 | -- | -- | 1 |
| 928 (21) | -- | -- | -- | 2 | -- | 1 | -- | -- | -- | 1 | -- | -- | -- | -- | -- | -- | -- | 1 | -- | -- |
| 929 (4) | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- |
| 930 (3) | -- | -- | -- | 1 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- |
| 931 (3) | -- | -- | -- | 1 | -- | -- | -- | -- | -- | -- | -- | -- | 1 | -- | -- | -- | -- | -- | -- | -- |
| 932 (17) | -- | -- | -- | -- | -- | -- | -- | -- | -- | 2 | -- | -- | 4 | -- | 6 | -- | -- | 1 | -- | -- |
| 934 (4) | -- | -- | -- | 4 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | 1 | -- | -- |
| 935 (19) | 5 | -- | 2 | -- | -- | -- | -- | 1 | -- | 1 | -- | 11 | 1 | -- | -- | -- | -- | -- | -- | -- |
| 936 (12) | -- | -- | 2 | -- | -- | -- | -- | 1 | -- | -- | -- | 2 | -- | -- | 4 | -- | -- | -- | -- | -- |
| 937 (28) | 1 | -- | 2 | -- | -- | -- | -- | 1 | -- | 11 | 4 | -- | -- | -- | -- | -- | -- | -- | -- | -- |
| 938 (10) | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- |
| 939 (5) | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- |
| 940 (6) | -- | -- | -- | -- | -- | -- | -- | 5 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- |
| 941 (35) | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | 2 | -- | 3 | -- | -- | -- | -- | 1 |
| 942 (46) | -- | -- | -- | 1 | -- | 2 | -- | -- | -- | 2 | -- | -- | -- | -- | -- | 1 | 1 | 2 | -- | 1 |
| 943 (35) | -- | -- | -- | 4 | -- | 1 | 4 | -- | -- | -- | -- | -- | -- | -- | -- | -- | 3 | -- | -- | 2 |
| 944 (8) | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | 1 | 1 | -- | -- | -- |
| 945 (12) | 3 | -- | -- | 3 | -- | 2 | -- | -- | -- | 3 | -- | -- | -- | -- | -- | 1 | -- | -- | -- | -- |
| 946 (36) | -- | -- | -- | -- | 19 | 2 | -- | 8 | -- | 10 | -- | -- | -- | -- | -- | -- | 2 | 2 | -- | -- |
| 947 (12) | -- | -- | -- | 1 | -- | 1 | 1 | -- | -- | -- | -- | -- | -- | -- | -- | -- | 1 | 2 | -- | -- |
| 948 (16) | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | 1 | 1 | -- | -- | 1 |
| 949 (19) | -- | 10 | -- | -- | -- | -- | -- | -- | 2 | -- | -- | -- | -- | -- | -- | -- | 1 | -- | -- | -- |
| 950 (16) | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | 1 | -- | -- | -- | 4 | -- | -- | -- |
| 951 (46) | -- | -- | -- | -- | 1 | -- | -- | -- | 1 | -- | -- | -- | -- | -- | -- | 2 | 2 | 1 | -- | 2 |

UNLABELLED TAXA: 912, 913, 933

Appendix 4 - cont.

| | 17 | 18.2 | | 20.1 | | 21.1 | | 22.1 | | 23 | 24.2 | | 25.2 | | 27.1 | 27.3 | | 29.1 | | 30 | |
|-----|----|------|----|------|------|------|------|------|----|------|------|------|------|----|------|------|----|------|----|----|----|
| | | 18.1 | 19 | 20.2 | 21.2 | 22.2 | 24.1 | 25.1 | 26 | 27.2 | 28.2 | 29.2 | 31 | | | | | | | | |
| 901 | -- | -- | -- | 1 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | 1 | -- | -- |
| 902 | -- | 6 | -- | -- | -- | 1 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | 1 | -- |
| 903 | -- | -- | -- | -- | -- | -- | -- | -- | 1 | -- | -- | -- | 1 | -- | 1 | -- | -- | -- | -- | -- | -- |
| 904 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- |
| 905 | -- | 4 | -- | 2 | -- | -- | -- | 1 | 3 | -- | -- | -- | -- | -- | -- | -- | -- | 1 | -- | -- | -- |
| 906 | 2 | -- | -- | 1 | -- | 2 | -- | 1 | 5 | 6 | 6 | 1 | -- | -- | 11 | 1 | 1 | -- | 8 | 1 | -- |
| 907 | -- | -- | -- | 1 | -- | 11 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | 1 | -- | 1 |
| 908 | -- | -- | -- | 7 | 2 | -- | -- | -- | 3 | 3 | -- | 1 | -- | 1 | -- | -- | -- | 8 | 1 | -- | 2 |
| 909 | 1 | 1 | 4 | -- | 3 | 2 | -- | 2 | 1 | -- | 1 | 3 | -- | -- | 1 | 1 | -- | -- | -- | 2 | -- |
| 910 | -- | -- | -- | -- | -- | -- | -- | -- | -- | 1 | 1 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- |
| 911 | -- | -- | -- | -- | -- | -- | -- | -- | -- | 1 | 1 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- |
| 914 | -- | -- | -- | -- | -- | -- | -- | -- | -- | 1 | 1 | -- | -- | -- | -- | -- | -- | -- | 1 | -- | -- |
| 915 | 4 | -- | 1 | -- | 1 | 1 | -- | -- | -- | -- | 1 | -- | -- | -- | 1 | 1 | -- | -- | 1 | -- | -- |
| 916 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- |
| 917 | -- | -- | -- | -- | -- | -- | -- | -- | -- | 1 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- |
| 918 | -- | -- | -- | 6 | -- | 4 | -- | -- | -- | -- | -- | -- | 6 | -- | 1 | 1 | -- | -- | -- | 3 | -- |
| 919 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | 2 | -- |
| 920 | -- | -- | -- | 1 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | 1 | -- | 2 | -- | -- | -- | -- |
| 921 | 1 | -- | 2 | -- | 1 | 4 | 11 | 1 | 1 | 2 | -- | -- | 1 | 2 | -- | -- | -- | 3 | -- | 5 | -- |
| 922 | -- | -- | 1 | 2 | 1 | -- | -- | 3 | 1 | 2 | -- | 2 | -- | 5 | -- | 1 | 1 | -- | 1 | 17 | -- |
| 923 | 5 | 3 | 1 | -- | -- | -- | -- | 1 | 2 | 1 | 1 | 1 | -- | 3 | 10 | -- | -- | 4 | -- | 1 | -- |
| 924 | -- | -- | -- | -- | -- | -- | -- | -- | -- | 1 | 1 | -- | -- | -- | -- | -- | 12 | -- | -- | 1 | -- |
| 925 | -- | -- | -- | -- | -- | -- | -- | -- | -- | 1 | 2 | -- | -- | -- | -- | -- | 12 | -- | -- | 1 | -- |
| 926 | -- | -- | -- | -- | 2 | -- | -- | 1 | -- | 1 | 1 | -- | -- | -- | -- | -- | -- | -- | -- | -- | 5 |
| 927 | -- | 1 | 1 | -- | 1 | -- | -- | 2 | 3 | -- | -- | -- | -- | -- | -- | -- | -- | -- | 1 | -- | -- |
| 928 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | 2 | -- | -- | -- |
| 929 | -- | 1 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | 1 | 1 | -- | -- | -- | -- | -- |
| 930 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- |
| 931 | -- | 1 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- |
| 932 | -- | -- | -- | -- | -- | -- | 1 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | 6 |
| 934 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- |
| 935 | -- | -- | 1 | -- | -- | -- | -- | 1 | -- | -- | -- | -- | -- | -- | -- | 1 | -- | -- | 1 | -- | 2 |
| 936 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | 1 | -- | -- |
| 937 | -- | -- | 2 | 2 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | 1 | -- | -- | 10 | -- | 1 |
| 938 | -- | 1 | -- | -- | 1 | -- | -- | -- | -- | -- | -- | -- | 1 | -- | 1 | -- | 1 | -- | -- | -- | -- |
| 939 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | 1 | -- | 1 | -- | -- | -- | -- | -- | -- |
| 940 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | 1 | -- | 1 | -- | -- | -- | -- | -- | -- | -- | -- |
| 941 | -- | 1 | -- | -- | -- | -- | -- | 1 | -- | 3 | -- | 6 | -- | -- | -- | -- | -- | -- | -- | -- | 6 |
| 942 | -- | 1 | -- | -- | -- | -- | -- | -- | -- | -- | 1 | 1 | -- | 1 | 1 | -- | 2 | -- | 1 | -- | -- |
| 943 | -- | 1 | -- | -- | -- | -- | -- | -- | -- | -- | -- | 1 | -- | 1 | 1 | -- | -- | -- | 1 | -- | -- |
| 944 | -- | -- | -- | 2 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- |
| 945 | -- | -- | -- | -- | 1 | -- | -- | -- | -- | -- | -- | 1 | -- | -- | -- | -- | -- | -- | -- | -- | -- |
| 946 | -- | -- | 1 | -- | 2 | -- | -- | 1 | -- | -- | -- | -- | -- | 1 | 1 | -- | -- | -- | 1 | -- | -- |
| 947 | 5 | -- | -- | 5 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | 2 | -- | -- | -- | -- | -- | -- |
| 948 | -- | -- | -- | -- | -- | -- | 1 | -- | -- | 1 | -- | 15 | -- | -- | -- | -- | 1 | -- | -- | -- | -- |
| 949 | -- | -- | 3 | -- | 1 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- |
| 950 | -- | -- | -- | -- | 2 | -- | -- | 4 | 3 | -- | 2 | -- | 1 | -- | -- | -- | -- | -- | -- | 1 | -- |
| 951 | -- | 2 | -- | -- | -- | -- | 1 | -- | -- | 1 | -- | 15 | 1 | -- | 1 | 1 | -- | 2 | -- | 1 | -- |

Appendix 4 - cont.

| | 32 | 35 | 36.2 | 37. | 39 | 41 | 42.2 | 43.2 | 44.2 | 45.2 | 47.1 | 48.1 | | | | | | | |
|-----|----|------|------|-----|----|------|------|------|------|------|------|------|----|----|----|----|----|----|----|
| | 33 | 36.1 | 36.3 | 38 | 40 | 42.1 | 43.1 | 44.1 | 45.1 | 46 | 47.2 | | | | | | | | |
| 901 | -- | -- | -- | 1 | -- | 3 | -- | -- | -- | -- | -- | -- | | | | | | | |
| 902 | -- | -- | -- | -- | -- | -- | 1 | -- | -- | -- | -- | -- | | | | | | | |
| 903 | -- | -- | 1 | -- | -- | -- | -- | -- | -- | -- | -- | -- | | | | | | | |
| 904 | -- | -- | -- | -- | 3 | -- | -- | -- | 1 | -- | -- | -- | | | | | | | |
| 905 | -- | -- | -- | -- | -- | 2 | 2 | -- | 2 | -- | -- | -- | | | | | | | |
| 906 | -- | 1 | -- | -- | 2 | 5 | -- | 3 | -- | 1 | -- | 1 | | | | | | | |
| 907 | 1 | -- | 1 | -- | -- | 1 | -- | 2 | -- | -- | -- | 1 | | | | | | | |
| 908 | 2 | -- | 1 | -- | -- | 1 | 1 | 3 | 1 | 2 | -- | -- | | | | | | | |
| 909 | -- | 1 | 1 | 4 | 1 | 2 | -- | 2 | -- | 3 | 5 | 2 | 1 | 3 | -- | 1 | -- | 2 | 1 |
| 910 | -- | -- | -- | -- | -- | -- | -- | -- | 1 | -- | -- | -- | -- | | | | | | |
| 911 | -- | -- | -- | -- | -- | -- | -- | -- | 1 | -- | -- | -- | -- | | | | | | |
| 914 | -- | -- | 1 | -- | -- | -- | -- | -- | -- | -- | -- | -- | 1 | | | | | | |
| 915 | -- | -- | 1 | 1 | -- | 1 | -- | 1 | 1 | 1 | 2 | -- | 1 | -- | -- | -- | -- | -- | 1 |
| 916 | -- | -- | -- | -- | -- | -- | -- | -- | 1 | -- | -- | -- | -- | | | | | | |
| 917 | -- | -- | 4 | 2 | -- | 1 | -- | -- | 3 | -- | -- | -- | -- | | | | | | |
| 918 | -- | -- | -- | -- | 1 | -- | -- | 2 | -- | 1 | -- | 2 | -- | -- | -- | -- | -- | -- | -- |
| 919 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | | | | | | |
| 920 | -- | -- | 2 | -- | -- | 6 | -- | -- | -- | -- | 2 | -- | -- | | | | | | |
| 921 | 4 | -- | 9 | -- | -- | 4 | -- | 1 | 1 | -- | 1 | -- | 15 | | | | | | |
| 922 | 1 | 1 | -- | 3 | -- | 1 | -- | 9 | 4 | 1 | 2 | -- | 1 | 4 | -- | -- | -- | 3 | |
| 923 | 3 | 1 | 6 | -- | -- | 1 | -- | -- | 1 | -- | 1 | -- | 1 | -- | -- | -- | -- | -- | -- |
| 924 | -- | -- | -- | -- | -- | -- | 1 | -- | 1 | -- | 1 | 1 | 1 | -- | -- | -- | -- | -- | 1 |
| 925 | -- | -- | -- | 3 | -- | -- | -- | 3 | -- | 3 | 1 | 1 | 6 | 4 | -- | -- | -- | -- | -- |
| 926 | 4 | -- | -- | -- | -- | -- | -- | -- | 2 | 1 | -- | 1 | -- | -- | -- | -- | -- | -- | -- |
| 927 | -- | 2 | -- | 1 | 1 | 2 | 1 | -- | 1 | -- | 1 | 1 | -- | -- | -- | -- | -- | 1 | -- |
| 928 | -- | -- | 1 | -- | 1 | -- | -- | 1 | -- | -- | 1 | 1 | 2 | -- | -- | 1 | -- | 1 | 1 |
| 929 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | 1 | -- | -- | -- | -- | -- | -- | -- |
| 930 | -- | -- | 1 | -- | -- | 2 | -- | -- | -- | 1 | -- | -- | 1 | -- | -- | -- | -- | -- | -- |
| 931 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | 1 | -- | -- | 1 | -- | -- | -- | -- | -- |
| 932 | 1 | -- | -- | -- | -- | 3 | -- | -- | -- | -- | 3 | 3 | -- | -- | -- | -- | -- | -- | -- |
| 934 | -- | -- | -- | -- | -- | 1 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- |
| 935 | 1 | -- | 1 | -- | -- | -- | -- | -- | 1 | -- | 1 | -- | -- | -- | -- | -- | -- | -- | -- |
| 936 | 1 | 1 | -- | -- | 4 | -- | 1 | -- | -- | 1 | -- | -- | -- | -- | -- | -- | -- | -- | -- |
| 937 | 1 | 2 | -- | 3 | -- | -- | -- | 1 | -- | 1 | -- | 5 | -- | 1 | -- | -- | -- | -- | -- |
| 938 | -- | -- | -- | -- | 3 | -- | 2 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | 2 | -- |
| 939 | -- | -- | -- | -- | -- | 1 | -- | -- | -- | 5 | -- | -- | 1 | -- | -- | -- | -- | -- | -- |
| 940 | -- | -- | -- | -- | 1 | -- | -- | 1 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- |
| 941 | 1 | 1 | 11 | -- | 1 | -- | 12 | -- | 2 | -- | 3 | -- | -- | 1 | -- | -- | 1 | -- | -- |
| 942 | -- | 1 | 1 | -- | 3 | -- | 1 | 1 | 2 | -- | -- | 1 | 2 | 1 | -- | -- | 1 | 1 | 1 |
| 943 | -- | 1 | -- | -- | -- | 2 | 17 | -- | 5 | -- | -- | -- | 1 | -- | -- | -- | 6 | -- | 2 |
| 944 | -- | -- | 1 | 1 | -- | 1 | -- | 1 | -- | -- | -- | 1 | -- | -- | -- | 1 | 5 | -- | -- |
| 945 | -- | -- | -- | -- | -- | 2 | -- | -- | -- | -- | -- | -- | 1 | -- | -- | -- | -- | -- | -- |
| 946 | -- | -- | -- | 1 | 1 | 1 | -- | 1 | 3 | -- | -- | 1 | 1 | -- | -- | 2 | 3 | -- | 1 |
| 947 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | 2 | -- | -- | 2 | -- | 2 | -- |
| 948 | -- | -- | -- | -- | -- | 1 | -- | 1 | -- | 1 | -- | 2 | 1 | 1 | 1 | 1 | -- | -- | -- |
| 949 | -- | -- | -- | -- | -- | -- | -- | 3 | -- | -- | -- | -- | -- | -- | -- | -- | 1 | 2 | -- |
| 950 | -- | -- | -- | -- | -- | 1 | -- | 1 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | 1 |
| 951 | -- | 3 | -- | -- | 1 | -- | 2 | 4 | 1 | -- | 1 | -- | 1 | 1 | -- | 1 | 1 | 3 | 2 |

Appendix 4 - cont.

| | 48.2 | 51.1 | 52.1 | 54 | 56 | 58.1 | 59 | 61.1 | 62 | 64 |
|-----|------|------|------|----|----|------|----|------|----|----|
| | 50 | 51.2 | 52.2 | 55 | 57 | 58.2 | 60 | 61.2 | 63 | |
| 901 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- |
| 902 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- |
| 903 | -- | -- | -- | 1 | -- | -- | 7 | -- | -- | -- |
| 904 | -- | -- | -- | 1 | -- | 3 | -- | -- | 1 | -- |
| 905 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- |
| 906 | 6 | -- | -- | -- | -- | 3 | -- | -- | 5 | 1 |
| 907 | -- | -- | -- | -- | -- | -- | -- | 1 | -- | -- |
| 908 | -- | 1 | 1 | -- | 2 | 2 | 2 | -- | 2 | -- |
| 909 | -- | 31 | -- | 1 | -- | 30 | 7 | 1 | 1 | 3 |
| 910 | -- | -- | -- | 1 | -- | -- | -- | -- | 2 | 5 |
| 911 | 1 | -- | -- | -- | -- | -- | -- | -- | 1 | 5 |
| 914 | -- | -- | -- | 6 | -- | -- | -- | -- | -- | -- |
| 915 | -- | 1 | -- | 3 | -- | 30 | 1 | -- | 1 | 1 |
| 916 | -- | -- | -- | 1 | 1 | -- | 4 | -- | -- | -- |
| 917 | -- | -- | -- | 3 | 4 | -- | -- | -- | 1 | 4 |
| 918 | -- | -- | -- | 2 | 2 | -- | -- | -- | 1 | -- |
| 919 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- |
| 920 | -- | -- | 1 | -- | -- | -- | -- | -- | 1 | 1 |
| 921 | -- | -- | -- | -- | 1 | -- | -- | 11 | -- | -- |
| 922 | -- | -- | 6 | 5 | -- | 1 | 1 | -- | -- | 1 |
| 923 | -- | -- | -- | -- | 1 | -- | -- | 1 | 4 | 1 |
| 924 | 1 | -- | -- | -- | -- | -- | -- | -- | -- | -- |
| 925 | 6 | -- | -- | -- | -- | -- | -- | -- | 1 | 1 |
| 926 | -- | -- | -- | -- | -- | -- | -- | -- | 2 | -- |
| 927 | -- | 31 | -- | -- | -- | 1 | 2 | 1 | 1 | 2 |
| 928 | 1 | -- | -- | -- | 2 | -- | 1 | 19 | 1 | 1 |
| 929 | -- | -- | -- | -- | 4 | -- | -- | -- | -- | -- |
| 930 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- |
| 931 | -- | -- | -- | -- | -- | -- | 1 | -- | -- | -- |
| 932 | 2 | -- | 1 | -- | -- | -- | -- | -- | -- | 1 |
| 934 | 1 | -- | -- | -- | -- | 1 | -- | -- | -- | -- |
| 935 | -- | -- | -- | -- | 2 | -- | -- | 3 | -- | -- |
| 936 | -- | -- | -- | -- | 2 | -- | 3 | -- | -- | -- |
| 937 | -- | -- | -- | -- | 3 | -- | 2 | 1 | -- | -- |
| 938 | 7 | -- | -- | -- | -- | -- | -- | -- | -- | 1 |
| 939 | -- | -- | 1 | 1 | -- | -- | -- | -- | -- | -- |
| 940 | -- | -- | 2 | 1 | -- | -- | -- | -- | -- | -- |
| 941 | -- | -- | 4 | 1 | -- | 4 | -- | 1 | 3 | -- |
| 942 | 2 | -- | 1 | 1 | -- | 1 | -- | 27 | 1 | 19 |
| 943 | -- | -- | -- | 1 | 6 | 7 | -- | -- | -- | 2 |
| 944 | -- | -- | -- | -- | -- | -- | 1 | -- | -- | -- |
| 945 | -- | -- | -- | -- | -- | 5 | -- | -- | -- | 2 |
| 946 | 2 | -- | -- | -- | -- | -- | -- | 1 | -- | 2 |
| 947 | 1 | -- | -- | -- | -- | -- | -- | -- | -- | 1 |
| 948 | -- | -- | 1 | -- | -- | -- | -- | 1 | -- | -- |
| 949 | -- | -- | 2 | 2 | -- | -- | 7 | -- | 1 | -- |
| 950 | -- | -- | 3 | 2 | -- | 3 | -- | 3 | -- | -- |
| 951 | 1 | -- | 2 | 1 | -- | -- | -- | 27 | 1 | 1 |

Appendix 5 Labels matrix derived from the reduced *Thyreodon/Euryophion* data set.

| | 6.1 | 8.1 | 12 | 13 | 14.1 | 16.2 | 18.2 | 19 | 20.1 | 21.1 | 21.2 | 26 | 27.1 | 27.2 | 30 | 31 | 32 | 33 | 36.1 | 37 | 39 | 41 | 43.1 | 44.1 | 44.2 | 45.1 | 59 | 62 | | | | | |
|----------|-----|-----|----|----|------|------|------|----|------|------|------|----|------|------|----|----|----|----|------|----|----|----|------|------|------|------|----|----|----|----|----|----|---|
| 901 (31) | -- | -- | 7 | -- | -- | 2 | 3 | 2 | -- | 11 | 1 | 2 | -- | 3 | 2 | -- | 1 | 1 | -- | 1 | -- | 4 | -- | 14 | 1 | 3 | -- | -- | -- | | | | |
| 902 (2) | -- | -- | -- | -- | -- | 1 | -- | -- | -- | 2 | -- | -- | 1 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | | | | |
| 903 (51) | 1 | 1 | 1 | 3 | 1 | 5 | 3 | 1 | 2 | -- | 5 | -- | 1 | 6 | -- | 14 | 2 | 1 | 2 | 2 | 1 | -- | 7 | 5 | 2 | -- | 1 | 3 | -- | 1 | 23 | 1 | |
| 904 (9) | -- | -- | -- | 1 | -- | 2 | 1 | 2 | -- | -- | -- | -- | -- | -- | -- | -- | -- | 1 | 1 | -- | -- | -- | -- | -- | 1 | 6 | -- | 1 | 2 | -- | -- | -- | |
| 907 (36) | -- | -- | 2 | 1 | -- | 4 | 1 | 1 | 4 | -- | 11 | 2 | 9 | -- | 3 | -- | 4 | 4 | -- | 2 | -- | 1 | 1 | 3 | 8 | 1 | -- | -- | -- | -- | -- | -- | |
| 908 (24) | 2 | 2 | -- | 4 | 1 | 2 | -- | -- | 10 | -- | -- | -- | 2 | -- | 2 | -- | 11 | -- | 2 | -- | -- | 2 | -- | 2 | -- | 2 | -- | 2 | -- | -- | 2 | -- | 2 |
| 921 (58) | 1 | 1 | 3 | 1 | 2 | 1 | 9 | 1 | 2 | 3 | 4 | 9 | 1 | 1 | 9 | 1 | 6 | 1 | 5 | 5 | 1 | 21 | -- | 1 | 14 | 3 | 2 | 1 | 1 | -- | 1 | -- | 1 |
| 935 (49) | 3 | 3 | 7 | 11 | 1 | -- | 3 | 1 | 1 | 1 | 3 | 4 | -- | 1 | -- | 3 | 2 | 9 | 1 | 1 | 3 | 1 | 1 | -- | 2 | -- | 1 | 1 | 1 | 3 | 23 | 3 | 3 |
| 936 (66) | 5 | 5 | 1 | -- | 1 | 12 | 5 | -- | 2 | 2 | 2 | 9 | -- | 5 | -- | 2 | 9 | 7 | 2 | 2 | 5 | 1 | 16 | 15 | 1 | -- | 2 | 2 | 9 | 5 | -- | 5 | 5 |
| 937 (53) | 3 | 3 | 7 | 2 | 2 | 3 | 1 | -- | 11 | 3 | -- | 1 | 1 | 3 | -- | 1 | 12 | 1 | 2 | -- | 3 | 21 | 1 | 1 | 3 | 1 | 2 | -- | 9 | 3 | 1 | 3 | 1 |

Appendix 6 Labels matrix derived from the reduced *Enicospilus/Staurooctonus* data set.

| | 1.1 | 3 | 5.1 | 6.1 | 7.2 | 12 | 13 | 14.2 | 15.2 | 16.2 | 17 | 18.2 | 19 | 20.1 | 21.1 | 22.1 | 24.1 | 25.2 | 27.2 | 29.2 | 31 | 35 | 36.2 | 37 | | | | | | | | | | | | | | | | | |
|-----------|-----|-----|-----|-----|-----|-----|----|------|------|------|----|------|------|------|------|------|------|------|------|------|------|----|------|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|---|---|---|
| | 1.2 | 4.1 | 5.2 | 4.1 | 5.2 | 7.2 | 13 | 15.1 | 16.2 | 18.1 | 19 | 20.1 | 21.1 | 22.1 | 24.2 | 27.1 | 27.3 | 30 | 33 | 36.1 | 36.3 | 39 | | | | | | | | | | | | | | | | | | | |
| 909 (139) | 4 | 16 | 1 | 17 | 11 | 4 | 28 | 2 | -- | 1 | 6 | 1 | 13 | 1 | -- | 9 | 4 | 1 | -- | 7 | 11 | -- | 1 | 1 | -- | 1 | -- | -- | 1 | 11 | 3 | 1 | 10 | 8 | | | | | | | |
| 910 (17) | -- | -- | -- | -- | -- | -- | -- | -- | 1 | -- | 3 | -- | -- | -- | -- | 5 | 3 | 3 | -- | -- | -- | -- | -- | -- | -- | 5 | -- | -- | -- | -- | -- | -- | -- | -- | -- | | | | | | |
| 911 (20) | -- | -- | -- | -- | -- | -- | -- | -- | 8 | -- | -- | -- | -- | -- | 5 | 3 | 3 | -- | 1 | 1 | -- | -- | -- | 5 | -- | -- | -- | -- | -- | -- | -- | -- | -- | 1 | -- | | | | | | |
| 913 (6) | -- | -- | -- | -- | -- | -- | -- | -- | -- | 3 | -- | -- | -- | -- | -- | 1 | -- | 1 | 1 | -- | -- | -- | -- | 1 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | | | | | | |
| 914 (10) | -- | 1 | -- | -- | -- | -- | -- | 1 | -- | -- | -- | -- | -- | -- | -- | 1 | 2 | -- | 1 | 1 | -- | 2 | -- | 1 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | | | | | | |
| 915 (40) | 1 | 1 | 2 | 1 | -- | 1 | 1 | -- | 1 | 7 | -- | 1 | 1 | -- | 1 | -- | 1 | 2 | 2 | 3 | -- | -- | 1 | 1 | -- | 1 | 1 | -- | 1 | 1 | -- | 1 | 1 | -- | 1 | 1 | | | | | |
| 916 (20) | 1 | 2 | -- | -- | -- | 1 | -- | 1 | 1 | -- | 1 | 1 | -- | 2 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | | | | | |
| 917 (20) | -- | 1 | -- | 2 | -- | -- | -- | -- | -- | -- | -- | 1 | -- | 4 | -- | 5 | 1 | 1 | -- | -- | -- | -- | -- | -- | -- | 6 | 3 | -- | 1 | -- | -- | -- | -- | -- | 1 | -- | | | | | |
| 918 (112) | 4 | 9 | 1 | 2 | 3 | 4 | -- | 4 | -- | 1 | 4 | 1 | -- | 1 | -- | 8 | 27 | 5 | 3 | 9 | -- | 1 | -- | 26 | 15 | 15 | -- | 22 | -- | -- | -- | -- | -- | 1 | -- | 2 | 6 | | | | |
| 919 (22) | 1 | 1 | 1 | 1 | -- | 1 | -- | 1 | -- | 1 | -- | 1 | 1 | 1 | 1 | -- | 1 | 1 | 1 | -- | 22 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | 1 | -- | | | | |
| 924 (21) | 1 | -- | -- | -- | -- | 1 | -- | 1 | 10 | -- | -- | -- | 1 | -- | 2 | -- | -- | 1 | 1 | -- | 11 | 2 | -- | 1 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | 1 | -- | | | | |
| 925 (52) | 6 | -- | -- | 1 | 6 | -- | -- | 1 | 3 | 1 | 3 | -- | 1 | -- | 2 | 3 | -- | -- | -- | 11 | 1 | -- | -- | 1 | 1 | 5 | 1 | 1 | -- | -- | -- | -- | -- | -- | 1 | 1 | | | | | |
| 926 (47) | -- | -- | 2 | -- | 2 | 9 | 10 | -- | -- | 6 | -- | -- | 4 | -- | 1 | 1 | -- | 1 | -- | 1 | 6 | -- | 19 | -- | -- | 5 | 4 | -- | -- | -- | -- | -- | -- | -- | -- | 4 | -- | | | | |
| 928 (19) | -- | 1 | -- | 1 | -- | 1 | -- | -- | 1 | -- | -- | -- | -- | -- | 1 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | 1 | -- | | | | |
| 929 (14) | -- | 1 | -- | -- | -- | 1 | -- | 1 | -- | -- | 11 | -- | -- | -- | -- | -- | -- | 2 | 2 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | 1 | -- | | | | |
| 930 (10) | 1 | -- | 1 | -- | -- | 1 | -- | 1 | -- | -- | 1 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | 1 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | 1 | -- | | | | |
| 931 (30) | -- | 4 | -- | 1 | -- | 1 | 8 | -- | 1 | -- | 2 | -- | 11 | -- | -- | -- | -- | 1 | 1 | -- | -- | -- | 3 | -- | -- | 1 | 2 | -- | -- | -- | -- | -- | -- | -- | 3 | -- | 1 | 2 | | | |
| 932 (31) | -- | -- | 1 | -- | 1 | 10 | 1 | -- | 1 | -- | 1 | -- | -- | 1 | -- | 3 | 3 | -- | -- | 1 | -- | 19 | -- | -- | -- | 1 | 2 | -- | -- | -- | -- | -- | -- | -- | -- | 1 | 2 | | | | |
| 934 (5) | -- | 4 | -- | -- | -- | -- | -- | -- | 1 | -- | -- | -- | 1 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | | | |
| 942 (18) | -- | 1 | -- | 1 | -- | 1 | -- | 1 | -- | 1 | -- | 1 | -- | 1 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | 1 | -- | 2 | | | |
| 943 (29) | -- | -- | 4 | -- | 3 | -- | -- | 1 | -- | 2 | 3 | -- | -- | 1 | 1 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | 1 | -- | 2 | | | |
| 944 (44) | 2 | -- | 1 | 1 | 1 | -- | 1 | -- | 3 | 2 | 2 | 1 | -- | 11 | 1 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | 16 | 2 | -- | -- | -- | -- | -- | -- | -- | -- | -- | 2 | -- | | | |
| 945 (46) | 5 | 1 | -- | 4 | 2 | 1 | -- | 5 | -- | 3 | 1 | 1 | -- | 1 | 1 | 2 | 1 | -- | 26 | 1 | 1 | -- | 1 | -- | 1 | 2 | -- | 2 | 1 | -- | -- | -- | -- | -- | -- | 1 | -- | 2 | 1 | | |
| 946 (29) | 1 | 1 | -- | 1 | 1 | -- | 28 | -- | -- | 1 | 1 | 1 | -- | 1 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | 1 | 1 | 2 | 1 | 1 |
| 947 (47) | 1 | 1 | -- | 4 | 1 | 1 | -- | 1 | 2 | -- | 15 | -- | 1 | 27 | 1 | 1 | 1 | -- | 1 | 2 | 2 | -- | 1 | -- | 1 | -- | 1 | -- | -- | -- | -- | -- | -- | -- | -- | 1 | -- | -- | 3 | 1 | |

Appendix 6 – cont.

| | 40 | 43.1 | | 44.1 | | 45.1 | | 46 | 47.2 | | 48.2 | | 52.2 | | 56 | 59 | 61.1 | | 62 | | | | | |
|-----|----|------|------|------|------|------|------|------|------|----|------|------|------|----|----|----|------|----|----|----|----|----|----|----|
| | | 42.2 | 43.2 | 44.2 | 45.2 | 47.1 | 48.1 | 52.1 | 55 | 57 | 60 | 61.2 | 64 | | | | | | | | | | | |
| 909 | 1 | 12 | 10 | 4 | 2 | 11 | -- | 3 | 2 | -- | 1 | 4 | 1 | 5 | 3 | -- | 28 | -- | 2 | -- | 1 | 2 | -- | -- |
| 910 | -- | -- | -- | -- | 3 | -- | -- | -- | -- | -- | -- | -- | -- | 1 | -- | -- | -- | -- | -- | -- | -- | -- | 5 | 5 |
| 911 | -- | -- | -- | -- | 3 | -- | -- | -- | -- | -- | 1 | 1 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | 3 | 5 |
| 913 | -- | -- | -- | 3 | -- | -- | -- | -- | -- | 1 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | 1 | -- |
| 914 | -- | -- | -- | -- | -- | -- | -- | -- | 3 | -- | -- | 1 | -- | -- | 6 | -- | -- | -- | -- | -- | -- | -- | -- | -- |
| 915 | -- | 1 | 1 | 2 | 2 | 6 | -- | 1 | -- | -- | -- | 1 | -- | 3 | -- | -- | 28 | -- | -- | -- | 1 | 1 | 1 | -- |
| 916 | 1 | 1 | -- | 1 | 1 | -- | -- | 1 | -- | -- | 1 | 1 | -- | 1 | 1 | -- | -- | 18 | 1 | -- | -- | 1 | -- | -- |
| 917 | -- | 1 | 7 | -- | 1 | 1 | -- | -- | -- | -- | -- | -- | -- | 2 | 3 | -- | -- | -- | -- | -- | -- | -- | -- | -- |
| 918 | 1 | 8 | -- | 5 | 4 | -- | -- | 5 | 2 | -- | 7 | 2 | 1 | 2 | 2 | 1 | -- | -- | 3 | -- | 3 | 3 | 1 | -- |
| 919 | -- | 1 | -- | -- | 1 | -- | -- | -- | -- | -- | 1 | -- | -- | -- | -- | -- | -- | -- | 1 | -- | 1 | 1 | -- | -- |
| 924 | -- | -- | 1 | 1 | 1 | 1 | 2 | -- | -- | -- | -- | 1 | 1 | -- | -- | -- | -- | -- | -- | -- | -- | -- | 1 | -- |
| 925 | -- | 1 | 15 | 1 | 2 | 10 | 12 | -- | -- | -- | 2 | 2 | 6 | -- | -- | -- | -- | -- | -- | -- | -- | -- | 4 | -- |
| 926 | 1 | -- | -- | 2 | 1 | -- | 7 | 1 | 1 | -- | -- | 4 | 1 | -- | -- | -- | 1 | -- | -- | -- | 2 | 2 | 1 | -- |
| 928 | 1 | -- | -- | 1 | 1 | 3 | -- | -- | 1 | -- | 1 | 1 | 1 | -- | -- | 2 | -- | -- | -- | 17 | 1 | 1 | -- | -- |
| 929 | -- | -- | -- | 1 | -- | -- | 1 | 1 | -- | -- | 1 | -- | -- | -- | 4 | -- | -- | -- | 1 | -- | -- | -- | -- | -- |
| 930 | -- | -- | -- | 1 | -- | -- | -- | -- | 2 | -- | -- | -- | -- | -- | 1 | -- | -- | -- | -- | -- | -- | 1 | 1 | -- |
| 931 | -- | -- | -- | 2 | 1 | -- | 11 | 1 | -- | -- | 3 | -- | -- | -- | 1 | -- | -- | -- | 3 | -- | 1 | 1 | -- | -- |
| 932 | 2 | -- | -- | -- | -- | -- | 2 | 2 | 2 | -- | -- | 2 | 2 | -- | -- | -- | -- | 4 | -- | -- | 1 | 1 | -- | -- |
| 934 | 1 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | 1 | -- | -- | -- | -- | 2 | -- | -- | -- | -- | -- | -- | -- |
| 942 | 1 | -- | -- | 1 | 1 | 1 | -- | -- | 1 | -- | 1 | 1 | 1 | -- | -- | 1 | -- | -- | -- | 17 | 1 | 1 | -- | -- |
| 943 | 4 | -- | -- | -- | 3 | -- | -- | -- | 2 | 15 | 1 | 1 | -- | 5 | 6 | -- | -- | 1 | -- | -- | -- | 1 | -- | -- |
| 944 | 3 | 2 | 1 | 1 | 1 | -- | -- | 1 | 2 | 15 | 1 | 3 | -- | 1 | 1 | -- | -- | 3 | -- | -- | -- | 5 | -- | -- |
| 945 | 4 | 1 | -- | -- | 1 | -- | -- | -- | 2 | -- | 1 | 2 | -- | 1 | 1 | 12 | -- | -- | -- | -- | 1 | 2 | -- | -- |
| 946 | 1 | 1 | 1 | 1 | 1 | 1 | -- | 1 | 1 | -- | 1 | 1 | 1 | -- | -- | -- | 1 | 1 | -- | -- | -- | -- | -- | -- |
| 947 | -- | 1 | -- | -- | 1 | -- | -- | -- | 3 | -- | 3 | 1 | 4 | 1 | 1 | -- | -- | -- | 1 | -- | 1 | 1 | 5 | -- |

Appendix 7 Character matrix for the HTUs.

| | 1.1 | 2 | 4.1 | 5.1 | 6.1 | 7.1 | 8.1 | 9 | 11 | 13 | 14.1 | 14.2 | 15.1 | 15.2 | 16.1 | 16.2 | 17 | 18.1 | 18.2 | 19 | 20.1 | 20.2 | 21.1 | 21.2 | 22.1 | 22.2 |
|------|------|------|------|------|------|------|-----|----|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|
| 960 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 |
| 961 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 |
| 962 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 |
| 963 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 |
| 964 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 965 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| 967 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 |
| 968 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 |
| 22.2 | 24.1 | 25.1 | 26 | 27.2 | 28.1 | 29.1 | 30 | 32 | 34 | 35 | 36.1 | 36.2 | 36.3 | 37 | 38 | 39 | 40 | 41 | 42.1 | 42.2 | 43.1 | 43.2 | 44.1 | 44.2 | | |
| 23 | 24.2 | 25.2 | 27.1 | 27.3 | 28.2 | 29.2 | 31 | 33 | 35 | 36.2 | 37 | 38 | 39 | 40 | 41 | 42.2 | 43.2 | 44.2 | | | | | | | | |
| 960 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 |
| 961 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 |
| 962 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 |
| 963 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 |
| 964 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 |
| 965 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 1 |
| 967 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 |
| 968 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 |
| 45.1 | 46 | 47.2 | 48.2 | 50 | 51.2 | 52.2 | 54 | 56 | 58.1 | 59 | 61.1 | 62 | 63 | 64 | | | | | | | | | | | | |
| 45.2 | 47.1 | 48.1 | 49 | 51.1 | 52.1 | 53 | 55 | 57 | 58.2 | 60 | 61.2 | 63 | | | | | | | | | | | | | | |
| 960 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 |
| 961 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 |
| 962 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 |
| 963 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 |
| 964 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| 965 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 |
| 967 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 |
| 968 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 |

Appendix 8 - cont.

| | 35 | 36.2 | 37 | 39 | 41 | 42.1 | 42.2 | 43.2 | 44.1 | 44.2 | 45.1 | 45.2 | 47.1 | 48.1 | 48.2 | 51.1 | 51.2 | 52.1 | 54 | 55 | 57 | 58.1 | 59 | 61.1 | 62 | 63 | | |
|-----|------|------|----|----|------|------|------|------|------|------|------|------|------|------|------|------|------|------|----|----|----|------|----|------|----|----|----|---|
| | 36.1 | 36.3 | 38 | 40 | 42.1 | 43.1 | 43.1 | 44.1 | 45.1 | 46 | | | | | | | | | | | | | | | | | | |
| 905 | -- | -- | -- | -- | 4 | 4 | -- | -- | 1 | 3 | -- | -- | -- | -- | -- | 1 | -- | -- | -- | -- | 1 | 1 | -- | -- | -- | 3 | | |
| 906 | 2 | -- | 1 | 3 | 7 | 2 | -- | 9 | 4 | 2 | 2 | -- | -- | 2 | 14 | -- | -- | 1 | -- | 1 | 6 | 2 | 1 | -- | 8 | 2 | | |
| 920 | -- | 25 | 2 | -- | 1 | 16 | 1 | 1 | -- | -- | 1 | 7 | -- | 13 | 1 | -- | 1 | 1 | -- | -- | 2 | -- | 2 | -- | 6 | 1 | | |
| 922 | -- | 25 | 4 | -- | 3 | 2 | 14 | 4 | -- | 19 | 3 | -- | -- | 2 | 8 | -- | 4 | 4 | -- | 2 | 3 | 2 | 1 | -- | 1 | 2 | 3 | |
| 923 | 8 | -- | 1 | -- | 3 | -- | 2 | -- | 1 | -- | 2 | 3 | -- | 1 | 3 | 2 | -- | 2 | -- | 2 | 5 | 2 | -- | 1 | 9 | 1 | 5 | |
| 927 | 1 | -- | 11 | 1 | -- | 2 | -- | -- | 1 | -- | -- | -- | -- | 2 | -- | 1 | 2 | -- | 1 | -- | 3 | 4 | -- | 2 | -- | 3 | 1 | |
| 938 | -- | -- | 10 | -- | 3 | -- | 1 | -- | 1 | 2 | -- | 2 | -- | 3 | -- | 14 | -- | 1 | -- | -- | -- | -- | 1 | 2 | -- | 1 | -- | |
| 939 | -- | -- | 2 | 2 | 1 | -- | -- | -- | -- | 17 | -- | -- | -- | 3 | -- | -- | 1 | 1 | -- | -- | 1 | -- | 1 | 1 | -- | 1 | -- | |
| 940 | -- | 1 | 7 | 1 | -- | 1 | 1 | -- | -- | -- | -- | -- | -- | 1 | -- | 2 | 1 | -- | 1 | -- | 1 | 1 | -- | -- | -- | -- | | |
| 941 | 14 | -- | 3 | -- | 6 | 12 | 1 | -- | 2 | 1 | 13 | -- | 1 | 1 | 3 | -- | 2 | 4 | 3 | -- | 9 | -- | 2 | 6 | -- | 3 | 1 | |
| 948 | -- | -- | -- | 2 | 1 | -- | 1 | -- | 2 | -- | 2 | -- | 8 | 1 | 1 | 3 | -- | 1 | -- | -- | 1 | -- | 2 | -- | 2 | -- | | |
| 949 | 1 | -- | 4 | -- | 1 | -- | 4 | -- | 4 | 2 | -- | 2 | -- | 6 | 4 | -- | 2 | 2 | -- | 20 | -- | -- | 4 | 1 | 1 | 2 | | |
| 950 | -- | 2 | -- | 1 | -- | 2 | -- | 1 | -- | 1 | -- | -- | -- | 1 | -- | 3 | 3 | -- | 7 | -- | -- | 4 | -- | 4 | -- | 1 | -- | |
| 951 | -- | -- | 1 | 5 | 4 | -- | 3 | -- | 1 | 1 | -- | 1 | 11 | 5 | -- | -- | 1 | -- | -- | -- | -- | -- | -- | -- | -- | 1 | -- | |
| 960 | 5 | -- | 3 | -- | -- | -- | -- | 2 | 1 | -- | -- | 2 | -- | 1 | -- | -- | -- | -- | -- | -- | -- | 2 | -- | -- | -- | 1 | -- | |
| 961 | -- | -- | -- | -- | 1 | -- | 1 | -- | 1 | -- | -- | -- | -- | 1 | 1 | 4 | -- | 22 | -- | -- | -- | -- | 1 | -- | 1 | 3 | 2 | |
| 962 | 4 | -- | 1 | -- | 1 | -- | 1 | -- | 1 | -- | 1 | -- | 1 | 2 | -- | 1 | 1 | -- | 20 | -- | -- | 1 | 2 | -- | -- | 1 | -- | |
| 963 | -- | 3 | -- | 7 | -- | 2 | -- | 2 | 1 | -- | -- | 3 | -- | 15 | 2 | 1 | 2 | 2 | 22 | 1 | -- | 1 | 1 | 2 | -- | 6 | 1 | 3 |
| 964 | -- | -- | -- | -- | 4 | -- | 1 | 2 | 7 | 12 | -- | 4 | 1 | 12 | -- | 2 | 2 | -- | 4 | -- | -- | 2 | -- | -- | -- | 6 | -- | |
| 965 | 1 | -- | 3 | -- | 1 | 1 | 3 | -- | 2 | 2 | 8 | 2 | -- | 3 | 14 | 3 | -- | -- | 4 | -- | 4 | -- | 2 | -- | -- | 2 | 2 | |
| 967 | -- | -- | -- | -- | 2 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | 2 | -- | 1 | 2 | -- | -- | -- | |
| 968 | -- | -- | -- | -- | 4 | -- | -- | -- | 1 | -- | -- | 1 | 3 | -- | 1 | -- | -- | -- | -- | -- | 1 | -- | 2 | -- | 5 | -- | -- | |

Appendix 9 Labels matrix derived from the *Euryophion* primary data matrix (Table 20).

| | 1.1 | 9 | 19 | 30 | 37 | 54 | 59 | 71 | 73 | 75 | | | | | | | | | |
|----------|-----|----|------|------|------|----|----|----|----|----|----|----|----|----|----|----|----|----|----|
| | 8.1 | 13 | 27.2 | 36.2 | 43.2 | 57 | 70 | 72 | 74 | | | | | | | | | | |
| 201 (6) | 2 | -- | -- | -- | 4 | -- | 1 | -- | -- | 2 | -- | -- | -- | 2 | -- | | | | |
| 202 (36) | 1 | 2 | 10 | 7 | 8 | 5 | 1 | 3 | 1 | 1 | 2 | 2 | 1 | 2 | 6 | 3 | 12 | 3 | |
| 203 (24) | -- | 6 | 10 | 1 | 1 | 5 | 3 | 4 | 2 | 3 | 3 | 6 | 2 | -- | -- | 1 | -- | 1 | -- |
| 204 (18) | 2 | 2 | 1 | 1 | 1 | -- | 2 | 6 | 1 | -- | 2 | 2 | 1 | 2 | -- | 1 | -- | 12 | -- |
| 205 (11) | -- | 3 | -- | -- | -- | 1 | 4 | 2 | -- | 3 | 4 | 3 | 2 | -- | -- | -- | -- | -- | -- |
| 206 (10) | -- | -- | -- | 2 | -- | -- | -- | 1 | 1 | 6 | -- | -- | -- | -- | 2 | 4 | 2 | -- | 2 |
| 207 (0) | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- |
| 208 (22) | -- | 1 | 1 | 5 | 8 | 2 | 1 | -- | 1 | -- | 1 | 1 | 11 | -- | 3 | 2 | 3 | 1 | 3 |

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